THE TAXONOMY OF THE GENUS *HETEROPELMA* WESMAEL (HYMENOPTERA : ICHNEUMONIDAE)

BY

IAN DAVID GAULD

Commonwealth Institute of Entomology

Pp. 153–219; 64 *Text-figures;* 3 *Charts;* 2 *Maps*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ENTOMOLOGY Vol. 34 No. 3
LONDON : 1976

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 34 *No.* 3 *of the Entomology series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Ent.).

ISSN 0524–6431

BRITISH MUSEUM (NATURAL HISTORY)

Issued 26 *August*, 1976 *Price* £5.60

THE TAXONOMY OF THE GENUS *HETEROPELMA* WESMAEL (HYMENOPTERA : ICHNEUMONIDAE)

By I. D. GAULD

CONTENTS

SYNOPSIS

The genus *Heteropelma* is defined and *Tanypelma* is included as a synonym of it. Seventeen species are recognized, four of which are new. Fifteen specific names are reduced to synonyms and one new combination is made. Six lectotype designations are made. All species are keyed and redescribed and notes on the distribution and biology, where known, are included. Intraspecific variation is discussed at length for some widely distributed species. The interspecific relationships are discussed from both phenetic and phylogenetic standpoints.

INTRODUCTION

Heteropelma is a moderate-sized genus belonging to the tribe Therionini of the subfamily Anomaloninae. Species have been recorded from all regions except the Ethiopian, but the majority of species occur on high ground in the Indo-Papuan region. Although host records are scarce certain species have repeatedly been recorded as parasites of pest species of Lepidoptera and thus several species of *Heteropelma* are insects of economic importance. As far as is known species of this genus are only parasitic on lepidopterous larvae, especially those of the Noctuoidea, Geometroidea and Sphingoidea. Oviposition is usually into early instar larvae.

The ichneumonid completes development in the host puparium and the adult invariably emerges by biting off the extreme anterior end of the host puparium.

Previous studies on this genus are mostly represented by scattered descriptions of new species and less often by keys to species of a particular region. Morley (1913*a*) included a key to world species represented in the collections of the British Museum (Natural History), but unfortunately he confused *Heteropelma* with other genera, thereby considerably reducing the value of his work. Schmiedeknecht (1936) and Uchida (1958) included useful keys to western and eastern Palaearctic species respectively. In these and all earlier works species now placed in *Heteropelma* were divided between two genera, *Heteropelma* and *Schizoloma*. As a result of examining some intermediate species Townes (1971) synonymized *Schizoloma* with *Heteropelma*.

A number of synonyms have been created because of the wide range of geographical distribution of several species. No attempt has been made by earlier authors to ascertain the range of variation occurring in the several species. The present paper is an attempt to delimit the known species more accurately and to give some insight into the range of variation, distribution and habits of members of this interesting genus.

NOMENCLATURAL SUMMARY

Townes and co-workers (1951; 1961; 1965) catalogued 27 species as either *Heteropelma* or *Schizoloma*. At the start of this work 25 were considered to be valid species, two having been reduced to synonyms by Gauld (1974). The nomenclatural changes made in the present work are summarized below.

HETEROPELMA Wesmael, 1849
- *Schizoloma* Wesmael, 1849
- *Tanypelma* Townes, 1971 **syn. n.**

calcator Wesmael, 1849

fulvitarse Cameron, 1899
- *reticulatum* Cameron, 1899 **syn. n.**
- *binghami* Cameron, 1907 **syn. n.**
- *grossator* Shestakov, 1923 **syn. n.**
- *perlongum* Cushman, 1937 **syn. n.**
- *panargis* Heinrich, 1953 **syn. n.**

elongatum Uchida, 1928

flaviscutellum Uchida, 1928
- *tarsale* Cushman, 1937 **syn. n.**

perornatum (Cameron), 1902

ocypeta **sp. n.**

celeno **sp. n.**

aello **sp. n.**

scaposum (Morley), 1913*a*
- *atrichiosoma* Morley, 1913*a*

flavitarse (Brullé), 1846
- *trichiosomum* Cameron, 1906

perniciosum (Turner), 1919

quodi (Vachal), 1907

savaiiense (Fullaway), 1940

townesi **sp. n.**

datanae Riley, 1888
flavicorne Brullé, 1846
fulvicorne Townes, 1945 **syn. n.**
nigricorne (Szépligeti), 1906 **comb. n.**
amictum (Fabricius), 1775
capitatum Desvignes, 1856 **syn. n.**
bucephalum Brauns, 1898
fulvicorne Cameron, 1899 **syn. n.**
tinctipenne Cameron, 1899 **syn. n.**
acheron Morley, 1913*a* **syn. n.**
acheron var. *scutellatum* Morley, 1913*b* **syn. n.**
sachalinensis Matsumura, 1918
crassicalx Enderlein, 1921 **syn. n.**
coreanum Uchida, 1928 **syn. n.**
amictum var. *nigricoxalis* Uchida, 1928
amictum var. *intermedium* Uchida, 1928
Nomen inquirendum
orbitale (Morley), 1913

The holotype and only known specimen of this species is deposited at the Museo Civico di Storia Naturale, Genoa. It has not been possible to examine this specimen. From the original description it would seem that this species is a synonym of *H. fulvitarse*.

MATERIALS EXAMINED AND METHODS USED

The following abbreviations have been used for depositories containing material which has been examined.

ANIC	Australian National Insect Collection, Canberra, Australia.
BMNH	British Museum (Natural History), London, England.
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.
DEI	Deutsches Entomologisches Institut, Eberswalde, D.D.R.
EIHU	Entomological Institute, Hokkaido University, Sapporo, Japan.
HKT	Townes Collection, Ann Arbor, Michigan, U.S.A.
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
IZPAN	Instytut Zoologiczny, Warsaw, Poland.
MNMH	Muséum National d'Histoire Naturelle, Paris, France.
QM	Queensland Museum, Fortitude Valley, Qld., Australia.
RSM	Royal Scottish Museum, Edinburgh, Scotland.
TM	Természettudományi Múzeum, Budapest, Hungary.
UM	University Museum, Oxford, England.
USNM	Smithsonian Institution, National Museum of Natural History, Washington D.C., U.S.A.
WAM	Western Australian Museum, Perth, W.A., Australia.
ZI	Zoological Institute, Leningrad, U.S.S.R.

For each species discussed a standardized format has been adopted. Whenever possible descriptions are based on type-material examined. Notes on intraspecific variation are given in a separate paragraph. Recorded hosts and synopses of recorded distribution, together with the appropriate references, are listed in separate paragraphs.

Drawings were made using a Wild M5 binocular microscope with a camera lucida attachment, except for figures of the genitalia which were made using a Watson 'Bactil' microscope in conjunction with a squared eyepiece.

The method of male genitalia preparation is particularly important as excessive maceration with caustic potash (KOH) causes undue distortion of the aedeagal membranes. The method described by Gauld (1976) for genitalia preparation was adhered to in the present study.

A number of indices adopted in an earlier work have been used in the present study. These are:

CI (cubital index of forewing) =

$$\frac{\text{length of } Cu_1 \text{ between } 1m\text{–}cu \text{ and } Cu_{1a}}{\text{length of } Cu_{1b}}$$

ICI (intercubital index of forewing) =

$$\frac{\text{length of } 2 + 3rm}{\text{length of } M \text{ between } 2 + 3rm \text{ and } 2m\text{–}cu}$$

MI (marginal index of forewing) =

$$\frac{\text{length of } Rs}{\text{length of } Rs + 2r}$$

NI (nervellar index of hindwing) =

$$\frac{\text{length of } Cu_1 \text{ between } cu\text{–}a \text{ and } M}{\text{length of } cu\text{–}a}$$

The measurement of wing veins follows the method outlined by Gauld (1976).

The abbreviations IOD and OOD were used respectively for the inter-ocellar and orbito-ocellar distances. Measurements of lower face were made taking the height as the distance between the mid clypeal apex and a mid point on a level with the lower margins of the antennal sockets, and the width as the minimum distance between the internal orbits.

Morphological nomenclature in this work follows that of Richards (1956) as interpreted for the Anomaloninae by Gauld (1976). The naming of genitalia structures follows that proposed by Peck (1937). The naming of microsculpture follows the system proposed by Eady (1968) and the larval terminology follows that of Short (1959).

HETEROPELMA Wesmael

Heteropelma Wesmael, 1849 : 120. Type-species: *Heteropelma calcator* Wesmael, 1849 : 120, by monotypy.

Schizoloma Wesmael, 1849 : 120. Type-species: *Ichneumon amictus* Fabricius, 1775 : 341, by monotypy.

Schizopoma Foerster, 1868 : 145, 220. [Unjustified emendation.]

Tanypelma Townes, 1971 : 157. Type-species: *Heteropelma fulvicorne* Townes, 1945 : 129 [=*Heteropelma datanae* Riley, 1888 : 177], by original designation. **Syn. n.**

Description. Eyes without pubescence, inner margins from subparallel to convergent

ventrally; occipital carina from close to posterior ocelli to widely separated from ocelli, rarely dorsally incomplete; frons with a weak to strong interantennal lamella. Antennae of moderate length, scape truncate, 1·3–1·7 times as long as pedicel; fourth flagellar segment 1·5–2·0 times as long as wide. Clypeus truncate, to rounded, sometimes with a pair of lateral swellings and apical clypeal margin reflexed; mandible bidentate, lower tooth always the shorter; labial palpi 4-segmented, cardo basally lobate. Genal carina reaching base of mandible.

Pronotum with a weak transverse furrow dorsally; posterior corner of pronotum partially occluding spiracular sclerite; lower anterior margin abruptly rounded without an apical concavity; notauli present, rarely absent. Mesopleuron dorsally usually rugose or coriaceous, lateroventrally punctate below a large speculum. Posterior transverse carina usually complete, rarely centrally absent.

Fore coxae smooth. Mid tibia usually bicalcarate, or in a Neotropical species with a single spur. Male hind tarsi swollen, 2nd segment usually with an impressed area ventrally which bears flattened microtrichia, or if rarely without this area then sometimes with microtrichia still present on ventral tarsal surface; hind claws usually geniculate and basally lobate, rarely simply curved.

Forewing with *Rs* weakly sinuate, 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separate. Cu_1 between *cu–a* and 1*m–cu*, 0·80–1·05 times as long as 1*m–cu*. Hindwing with 12–18 hamuli on vein R_1; distal abscissa of Cu_1 always present.

Propodeum reticulate, spiracle 2·50–3·50 times as long as broad; propodeum occasionally with conspicuous lateral protuberances. Gaster elongate, basal segments slender.

♀ genitalia. Valvula 3 a little longer than apical depth of gaster; apex of ovipositor strongly constricted, extreme apex decurved; conspicuous sclerotized nodus present (Text-fig. 55).

Ovarian egg obovate, dorsally flattened, bearing an obvious mushroom-like protuberance (the sucker of Iwata, 1958) that is basally extended anteriorly to form a thickened ridge or pair of ridges on the outer surface of the egg (Text-figs 56–64).

♂ genitalia. Single syntergum present; 9th abdominal sternite from almost quadrate to distinctly transverse; gonosquamae short, usually acute apically. Gonolacinia distally abruptly angled about 90°, teeth short to vestigial; basal apodeme angled at about 20° to the axis of the gonolacinia, reaching at least 0·65 of length of basivolsellar strut. Distivolsella slender, basally less than 0·5 times as broad as long, distally more or less swollen; teeth generally arranged diagonally on clasping face often with cluster on upper inner face, sometimes with smaller teeth distributed all over inner face. Aedeagal paramere proximally rounded, weakly spatulate or acute. Aedeagus in profile more or less sinuate, usually apically bilobate with obvious lateral sclerotized region; ventral membranous area bearing spines in specific patterns.

IMMATURE STAGES. Only the first instar larva of one species, *H. calcator*, has been described (Plotnikov, 1914). The characteristic features of this larva are the elongate caudal appendage and presence of a small mouth with minute mandibles. The second instar larva resembles the first but has a much shorter caudal appendage.

The final instar larvae of four species, *H. amictum*, *H. calcator*, *H. scaposum* and *H. datanae*, have been examined. The cephalic capsule of species of this genus is characterized by the broad pleurostoma and epistoma, short hypostoma and by having the labral sensilla arranged in two separate clusters. Most species were found to have the lateral ends of the hypostoma decurved, unlike species of *Therion* which have the hypostoma laterally straight. However, one species, *H. scaposum*, was observed to have the hypostoma laterally straight (Text-fig. 37). *H. amictum* and *H. datanae* were observed to have the ventral part of the labial sclerite lightly sclerotized. In the larva of *H. scaposum* this sclerite is medio-ventrally extremely weakly defined. *H. calcator* was observed to be more variable. Some specimens have been found with the labial sclerite medio-ventrally sclerotized whilst Short

(1970) observed that *H. calcator* has the ventral part of the labial sclerite incomplete and not sclerotized (Text-fig. 36).

Discussion of some characters. In previous work (Gauld, 1976) it was stated that *Heteropelma* species invariably have the inner margins of the orbits convergent ventrally and have the posterior transverse carina of the mesosternum complete. Exceptions have now been found to both these generalizations. A Papuan species, described below, was found to have the posterior transverse carina of the mesosternum centrally incomplete and *H. nigricorne* was observed to have the lower face subquadrate with the inner orbits extremely weakly convergent ventrally.

This recent advance in the state of knowledge of this group makes it desirable to modify couplet 7 in the key to genera included by Gauld (1976). The amended couplet should read:

7 (6) Posterior transverse carina of mesosternum interrupted before each mid coxa; propodeum simple without lateral protuberances; lower face at narrowest point at least 0·85 times as broad as high; hind tarsal claws simply curved; ♂ with proximal apodeme of gonolacinia angled at 40° to gonolaciniar axis and less than 0.3 times as long as basivolsellar strut. Holarctic, extending into the Neotropics as far as about 20°N and into the Oriental region as far as New Guinea . . . . . ***THERION*** Curtis

– Posterior transverse carina of mesosternum complete, or if rarely incomplete then propodeum with conspicuous lateral protuberances; lower face less than 0·9 times as broad as high; hind tarsal claws often geniculate; ♂ with proximal apodeme of gonolacinia angled at about 20° to gonolaciniar axis and more than 0·6 times as long as basivolsellar strut. All regions except Ethiopian ***HETEROPELMA*** Wesmael

Couplet 8 is made redundant as, for reasons given below, *Tanypelma* has now been included as a synonym of *Heteropelma*.

In the work cited above, *Tanypelma* was included as a separate genus, but it was stated that this genus appeared to have close affinities with *Heteropelma*, and that its status might need reconsideration. Recently a number of additional species have been studied and as a result the status of *Tanypelma* has been re-examined.

The differences previously used for separating the two genera are tabulated below.

HETEROPELMA	*TANYPELMA*
Scutellum in profile flat (Text-fig. 24).	Scutellum in profile convex (Text-fig. 26).
NI less than 0·60.	NI greater than 0·80.
2nd hind tarsal segment of ♂ usually with an impressed area ventrally.	2nd hind tarsal segment of ♂ without an impressed area ventrally.
Lower face elongate.	Lower face subquadrate.

Most species of *Heteropelma* were observed to have the scutellum flattened and more or less longitudinally concave. Species referred to *Tanypelma* were observed to have the scutellum more or less strongly convex. However, two species, *H. quodi* and *H. savaiiense*, were found to have a weakly swollen scutellum intermediate between that of typical *Heteropelma* and *Tanypelma* (Text-fig. 25).

The differences in the range of variation of NI previously considered useful for effecting generic separation have been invalidated by the examination of additional

material. A Brazilian species, *H. townesi*, resembles *Heteropelma* in most features (i.e. has the ♂ hind tarsi impressed, scutellum flat, etc.) but has NI between 0·70 and 0·90 thus overlapping the range of *Tanypelma*. *H. savaiiense* was observed to have NI equal to 0·70. The range of values of NI for *Heteropelma* must now be accepted to be 0·20–0·90 and it is therefore no longer possible to use this character to separate *Heteropelma* from *Tanypelma*.

The majority of species of *Heteropelma* have the 2nd hind tarsal segment of the male ventrally impressed. Two species of *Heteropelma* do not have such an impression present and thus resemble *Tanypelma*.

Tanypelma species have the lower face subquadrate whereas most species of *Heteropelma* have the lower face elongate. However, *H. nigricorne* has been found to have the lower face subquadrate.

Bearing in mind the combination of characters exhibited by *Tanypelma datanae* (the only species referable to the genus), it is apparent that this species differs somewhat from the majority of species of *Heteropelma*. Five other species differ as much, or more, from the majority of *Heteropelma* species as does *T. datanae* (Chart 2), but it would not be concomitant with the classificatory criteria adopted for the Therionini as a whole to accord each of these species separate generic status.

One may conclude that, because of the presence of intermediate species, and the existence of a much greater range of morphological variation than was presupposed to occur within the genus *Heteropelma*, the status of *Tanypelma* as a distinct genus can no longer be considered to be justifiable. It is suggested therefore that it should be included as a synonym of *Heteropelma* as formally stated above.

In earlier works (that is all pre-1970 literature) *Heteropelma* and *Schizoloma* were treated as distinct genera on account of differences in the form of the clypeus and ratio of hind basitarsus to 2nd tarsal segment. Numerous intermediate forms between the two extremes of clypeal shape have been found (this is discussed further under the variation occurring in *H. amictum*). There is a considerable range of variation in the values of the hind tarsal ratios between species. As the ranges of several species overlap, the apparent difference between *Heteropelma* and *Schizoloma* is invalidated. The author therefore concurs with the opinion of Townes (1971) who placed *Schizoloma* as a synonym of *Heteropelma*.

The characteristic form of the ovarian eggs of species of this genus was described by Iwata (1958). It has been possible to examine the ovarian eggs of six species, *H. fulvitarse*, *H. calcator*, *H. perornatum*, *H. amictum*, *H. celeno* and *H. scaposum* (Text-figs 56–64). The characteristic pedicel, called a sucker by Iwata, cannot in fact function as such, as the end is clearly distally convex (Text-fig. 56). The function of the pedicel is apparently to secure the egg to a suitable position within the host (Tothill, 1922). It is suggested that, rather than acting as a sucker, the membranous flange surrounding the distal apex of the pedicel functions as a barb preventing the pedicel from becoming dislodged from the tissue in which it had been embedded.

Specific differences were found in the form of the pedicel and its basal insertion. In the majority of species the pedicel was positioned postero-dorsally but in *H. scaposum* a particularly conspicuous pedicel was positioned medio-dorsally. The

exact form of the anterior constricted region of the egg was observed to be variable. In immature eggs this region was extended into an elongate spout, whilst in more mature eggs the size of this spout was considerably reduced. The eggs of *H. scaposum* were not observed to have a spout.

Systematic position of the genus. *Heteropelma* is apparently related to *Habronyx* (*Habronyx*), *Therion* and less closely to *Trichomma*. All these genera share a number of features in common including specialized eggs, a slender distally swollen distivolsella and broad larval pleurostomae. The latter two genera have like *Heteropelma* the gonolacinial apodeme formed from a sclerotized portion of the outer margin of the gonolacinia. Gauld (1976) included a full discussion of the possible evolutionary significance of these and other characters but was unable to satisfactorily relate *Heteropelma* to *Therion* on account of marked differences in the form of the aedeagus. A Papuan species, *H. celeno*, was observed to have an aedeagus intermediate in structure between those of typical *Heteropelma* and *Therion*. A second and closely related Papuan species, *H. aello*, was observed to have an incomplete posterior transverse mesosternal carina, a characteristic of *Therion* rather than *Heteropelma*. However, in all other features these species were clearly referable to *Heteropelma*. It is now considered possible that *Heteropelma* may have evolved from a common ancestor with *Therion*, and that these two Papuan species represent the closest known species to this hypothetical ancestor.

Key to species of *HETEROPELMA*

1 Propodeum with a pair of lateral thorn-like projections (Text-figs 33, 34); pronotum without a well developed hook on lower anterior margin (Text-fig. 29); gaster black, thorax predominantly brick red.
Papuan species 2

– Propodeum without thorn-like lateral projections; pronotum with moderately well developed hook on lower anterior margin (Text-figs 27, 28); gaster and thorax variously coloured, the latter usually darker than the former 3

2 Face with elongate black pubescence; lateral projection of propodeum very acute (Text-fig. 34); posterior transverse carina of mesosternum centrally absent
aello sp. n. (p. 176)

– Face with short pale pubescence; lateral projection of propodeum blunt (Text-fig. 33); posterior transverse carina of mesosternum complete . ***celeno*** sp. n. (p. 175)

3 Forewing with abscissa of *M* between 2 + 3*rm* and 2*m–cu* more than 3·0 times as long as 2 + 3*rm* (Text-fig. 39); an entirely brick red species.
Samoan Islands . . . . . ***savaiiense*** (Fullaway) (p. 183)

– Forewing with abscissa of *M* between 2 + 3*rm* and 2*m–cu* less than 2·5 times as long as 2 + 3*rm* (Text-fig. 40); insect blackish marked on thorax or hind legs . . 4

4 Marginal cell elongate, *Rs* more than 2·0 times as long as *Rs* + 2*r* (Text-fig. 40); hind trochanter equal to or longer than trochantellus ventrally; Cu_1 between 1*m–cu* and Cu_{1a} less than 0·6 times as long as Cu_{1b}; mid tibia unicalcarate.
Neotropical species . . . . . ***townesi*** sp. n. (p. 184)

– Marginal cell shorter, *Rs* less than 1·9 times as long as *Rs* + 2*r*; hind trochanter ventrally shorter than trochantellus; Cu_1 between 1*m–cu* and Cu_{1a} more than 0·6 times as long as Cu_{1b}; mid tarsi bicalcarate, rarely with inner spur very reduced . 5

5 Scutellum in profile swollen (Text-fig. 26); hind wing with NI greater than 0·70; male without either an impressed area or flattened microtrichia on 2nd hind tarsal segment.
Nearctic species . . . . . ***datanae*** Riley (p. 185)
– Scutellum in profile flat (Text-figs 24, 25); hind wing usually with NI less than 0·65; male with either an impressed area or flattened microtrichia or both on ventral surface of 2nd hind tarsal segment 6
6 Hind basitarsus bicoloured, proximally black, distally yellowish; Australasian species 7
– Hind basitarsus unicolorous yellow, very rarely with indistinct infuscation at extreme proximal end; Palaearctic or Oriental species 10
7 Hind legs except tarsi almost entirely black; wings strongly infumate; tegulae black; New Caledonia . . . . . ***quodi*** (Vachal) (p. 182)
– Hind legs with at least femora broadly red marked; wings hyaline or very weakly infumate; tegulae often yellow; Australian species 8
8 Hind tarsal claws weakly curved, without a basal lamella (Text-fig. 31); lower face usually black marked, always with elongate black pubescence; hind coxa ventrally with dense elongate pubescence; hind ocelli separated from occipital carina by a distance about equal to an ocellar diameter and flagellum with 60+ segments.
Large species, forewing length 12–16 mm; Tasmania and southern Australia ***flavitarse*** (Brullé) (p. 180)
– Hind tarsal claws geniculate with a strong basal lobe or lamella (Text-fig. 30); lower face usually entirely yellowish with pallid pubescence; hind coxa ventrally with short sparse pubescence; hind ocelli separated from occipital carina by a distance greater than 1·2 times the ocellar diameter or flagellum with less than 58 segments or both 9
9 Thorax mainly black; dorsum of tergite 3 0·90 times or more as long as tergite 4; common species . . . . . ***scaposum*** (Morley) (p. 177)
– Thorax almost entirely reddish brown, only black marked dorsally and ventrally; dorsum of tergite 3 0·80 times or less as long as tergite 4; rare species ***perniciosum*** (Turner) (p. 181)
10 Hind basitarsus more than 3·00 times as long as 2nd tarsal segment; clypeus evenly rounded, in profile not swollen 11
– Hind basitarsus less than 2·80 times as long as 2nd tarsal segment; clypeus with a weakly to very strongly produced pair of lateral swellings, in profile convex or apically reflexed (Text-figs 16–18) 16
11 Mid tibia with spurs extremely inequal, the inner spur vestigial, less than 0·25 times as long as the outer (Text-fig. 35); occipital carina separated from posterior ocelli by more than 1·30 times ocellar diameter (Text-fig. 10).
Thorax highly polished; Malaysian species . . . ***ocypeta*** sp. n. (p. 174)
– Mid tibia with subequal to inequal spurs, the inner spur at the very least 0·45 times as long as the outer; occipital carina separated from posterior ocelli by less than 1·20 times ocellar diameter (Text-figs 1–6) 12
12 Mid tibial spurs inequal, the longer about 2·0 times as long as the shorter and the interantennal lamella vestigial (Text-fig. 23); scutellum yellow; flagellum with about 45 segments; male with hind basitarsus and 2nd tarsal segment confluent in outline, the latter without an impressed ventral area (Text-fig. 38)
Japan, Taiwan. . . . . ***flaviscutellum*** Uchida (p. 170)
– Mid tibial spurs generally subequal, the longer less than 1·5 times as long as the shorter or if very rarely with the longer 1·6–1·8 times as long as the shorter then the interantennal lamella is strongly developed (Text-fig. 20); interantennal lamella moderately to strongly developed (Text-figs 20–22); scutellum usually black; flagellum often with more than 46 segments; male with 2nd hind tarsal

segment in outline discrete from basitarsus, and often with a ventral impressed area on the former (Text-fig. 41) 13

13 Head posteriorly very strongly narrowed (Text-fig. 6); occipital carina medio-dorsally flattened with a more or less distinct median dip; flagellum with about 55 segments; pronotum with postero-dorsal half smooth with scattered punctures (Text-fig. 27).
Borneo . . . . . ***perornatum*** (Cameron) (p. 173)

– Head less strongly narrowed (Text-figs 1–5); occipital carina medio-dorsally usually convex, rarely slightly flattened but then with flagellum with 60+ segments; pronotum with postero-dorsal half coriaceous 14

14 Head when viewed dorsally with genae broad and weakly constricted (Text-figs 3, 4); flagellum with 48 or less segments; hind coxa usually entirely black, rarely in some east European specimens with reddish marks.
Palaearctic; coniferous woodlands . . . ***calcator*** Wesmael (p. 164)

– Head when viewed dorsally with genae not exactly as above, somewhat more posteriorly constricted (Text-figs 1, 2, 5); flagellum with 50+ segments; hind coxa entirely red or with extreme proximal margin black. 15

15 Hind basitarsus more than 4·8 times as long as 2nd tarsus; male without an impressed area on 2nd hind tarsal segment; propodeum dorsally about as long as broad; interantennal lamella triangular in profile (Text-fig. 22); flagellum with 60+ segments; eastern Palaearctic . . . . ***elongatum*** Uchida (p. 169)

– Hind basitarsus less than 4·50 times (usually less than 4·30 times) as long as 2nd tarsus; male with an impressed area on 2nd hind tarsal segment; propodeum dorsally broader than long; interantennal lamella trapezoidal in profile (Text-fig. 20); Oriental and Palaearctic . . . . ***fulvitarse*** Cameron (p. 167)

16 Lower face subquadrate, about 0·80 times as broad as high (Text-fig. 14); IOD 0·6 times as long as OOD; vertex immaculately black; flagellum blackish; clypeus with weak lateral protruberances.
S. India . . . . . ***nigricorne*** (Szépligeti) (p. 187)

– Lower face elongate, less than 0·70 times as broad as high (Text-fig. 16); IOD 0·65 or more times as long as OOD; vertex with yellow marks . ***amictum*** (Fabricius) (p. 188)

DESCRIPTIONS OF SPECIES

Heteropelma calcator Wesmael

(Text-figs 3, 4, 19, 36, 48, 59, 63)

Heteropelma calcator Wesmael, 1849 : 120. Syntypes, Belgium (IRSNB) [not examined].
Heteropelma calcator Wesmael; Morley, 1913*a* : 69.
Heteropelma calcator Wesmael; Plotnikov, 1914 : 34.
Heteropelma calcator Wesmael; Morley, 1915 : 231.
Heteropelma calcator Wesmael; Uchida, 1928 : 237.
Heteropelma calcator Wesmael; Meyer, 1935 : 60.
Heteropelma calcator Wesmael; Schmiedeknecht, 1935 : 62.
Heteropelma calcator Wesmael; Uchida, 1958 : 94.
Heteropelma calcator Wesmael; Iwata, 1958 : 70.
Heteropelma calcator Wesmael; Townes, Momoi & Townes, 1965 : 382.
Heteropelma calcator Wesmael; Constantineanu & Petçu, 1969 : 93.
Heteropelma calcator Wesmael; Gauld, 1973 : 304.

The type-material of this species was being studied by Dr Schnee (August, 1975) who was preparing a work on European Anomaloninae.

Description. Lower face 0·60–0·70 times as broad as high; clypeus apically simply convex, in profile almost flat; mandibles twisted about 15°, the upper tooth about 2·00 times as long as lower; IOD 1·10–1·40 times as long as OOD; posterior ocelli separated from occipital carina by about maximum ocellar diameter. Head rather weakly constricted posteriorly, vertex punctate to coriaceous; occipital carina medio-dorsally usually evenly rounded, sometimes flattened. Flagellum of moderate length, 43- to 48-segmented; 1st flagellar segment 2·0–2·3 times as long as 2nd; interantennal lamella strong, in profile almost square. Face with long, yellowish brown pubescence.

Pronotum coriaceous, anterior hook strong. Mesoscutum coriaceous, laterally punctate; notauli strong, reaching beyond centre of mesoscutum; mesoscutal pubescence long, yellowish brown in colour. Mesopleuron dorsally rugose, lateroventrally punctate; epicnemial carina reaching above centre of mesopleuron, bowed so that upper end reaches anterior pleural margin; sternaulus weak. Scutellum usually longitudinally concave, slightly elongate, coriaceous. Posterior transverse carina of mesosternum complete. Propodeum reticulate, without lateral projections, ventrally sculptured; propodeum dorsally 0·70–0·80 times as long as broad.

Mid tibial spurs subequal, the outer about 1·10 times as long as inner. Hind leg with basitarsus 0·50–0·60 times as long as tibia, 3·40–3·80 times as long as 2nd tarsal segment; 2nd tarsal segment 1·90–2·20 times as long as 3rd; trochanter 0·80–0·90 times as long as trochantellus ventrally; hind tarsal claw geniculate, basally strongly lobate. ♂ with 2nd hind tarsal segment with an impressed ventral area.

Wings very weakly infumate; CI = 0·55–0·80; MI = 1·75–1·90; ICI = 0·90–1·40; NI = 0·45–0·50. Forewing length 8–11 mm.

Gaster with tergite 2 2·20–2·40 times as long as tergite 3; ♀ with ovipositor about 0·60 times as long as tergite 2.

♂ genitalia. Distivolsella with spines arranged in apical cluster and with a short row of double spines on ventral region. Aedeagus in profile apically subequally bilobate; lateral sclerotized region apically dilated, indistinctly delineated.

Head black, lower face and orbital marks yellow; flagellum reddish, proximally black. Thorax black, tegulae reddish. Legs reddish brown, coxae usually black, rarely reddish tinged or occasionally entirely red distally; distal 0·3 of hind tibia black, hind tarsi yellow. Gaster reddish, black marked on dorsal margin of tergite 2 and with terminal segments infuscate.

Variation. This species exhibits less variation than the related species *H. fulvitarse* although it extends over a large range. Specimens from eastern Europe occasionally have the hind coxae distally red but all such specimens were observed to have the coxae black at extreme proximal ends.

Remarks. This is one of the commonest Palaearctic species of Anomaloninae, about which a very considerable body of literature has accumulated. An excellent account of the biology and descriptions of the larval stages were included by Plotnikov (1914). The ovarian egg was described by Iwata (1958). This species is a well known parasite of *Bupalus piniaria* (L.) and because this moth is an important pest of conifer plantations a number of workers have studied the host-parasite interrelationship (Ljungdahl, 1916; Ritzema, 1920; Seitner, 1922; Sitowski, 1922; Barbey, 1927; Gornitz, 1931; Steiner, 1931; Friedrichs, Schaerffenberg & Sturm, 1941; Hedqvist, 1949 and Malysheva, 1960; 1962).

The following brief account of adult behaviour is based on personal observation of two populations, one at Cannock Chase, Staffordshire, England and a second at Craigen Darroch, Grampian, Scotland.

H. calcator is generally associated with *Pinus* woodlands. It seems to prefer

areas in which there are many young trees (2–3 m high) or in which taller trees (4–5 m) are widely spaced. Males appear in mid July and specimens of both sexes are most common in mid August.

In flight both sexes adopt a very characteristic attitude, flying with antennae outstretched, hind legs fully extended at about 30° to the axis of the body and with the slender gaster elevated at about 15°. A considerable amount of the flight path is in the vertical plane, close to the conifer foliage.

At night and during periods of inclement weather both sexes rest on conifer twigs. At rest they elevate the gaster at an angle approximately the same as that subtended by the leaves to the twigs. Thus the insect renders itself very inconspicuous.

Males adopt a characteristically rapid flight in clearings, rising vertically and sinking, with the conspicuous hind tarsi outstretched. Two or three males behaving so together have been seen, but no evidence for aggregate male displays exists. Whether this behaviour is some form of pre-copulatory sexual display is not known.

The female searches for prospective hosts on the wing, and alights only for the briefest moments to preen the antennae and wings. Having located a suitable host (usually the early instar larvae of *B. piniaria*) the female alights, reflexes the ovipositor forward and then oviposits, after which she resumes flight. The reflexing of the ovipositor serves to move an egg from the ovipositor base to an expanded chamber immediately proximal to the nodus. During this reflexing the 1st valvulae are retracted relative to the 2nd valvulae, and the valvilli (a pair of minute flanges of tissue positioned on the distal internal faces of the 1st valvulae, vide Gauld, 1976) engage the egg. As the 1st valvulae slide along the 2nd to regain their resting position the egg is forced down the lacuna of the ovipositor by the valvilli. Thus when the ovipositor is inserted into the lepidopterous larva an egg is already positioned near the apex.

Observation of acts of oviposition were too infrequent to permit any reliable inferences being made about the position of insertion of the ovipositor into the host.

H. calcator is undoubtedly closely related to the Oriental species *H. fulvitarse* which apparently occupies a similar ecological niche in the Oriental region. The two species are morphologically rather similar but it seems possible to separate the two by differences in head shape (Text-figs 1–4) and usually by differences in coxal coloration. Whether or not these differences will prove to be reliable when the fauna of western and central Asia is better known is a matter of great interest.

Host records. Other than *B. piniaria* which is referred to above, this species has been recorded as a parasite of *Panolis flammea* (Denis & Schiffermüller) (Meyer, 1935; Schmiedeknecht, 1935), *Anarta myrtilli* (L.) (Schmiedeknecht, 1935), *Bena prasinana* (L.) (Morley, 1915; Meyer, 1935).

Distribution (Map 1). This species has been recorded from most European countries (Schmiedeknecht, 1935), but is perhaps absent in the south as Ceballos (1963) failed to find it in Spain. Meyer (1935) recorded this species from many localities in the U.S.S.R. Uchida (1958) recorded this species from eastern U.S.S.R., China, Korea and Japan.

MATERIAL EXAMINED.

BELGIUM: 1 ♀, no further data (BMNH). GERMANY: 4♀, 2♂, no further data (BMNH). GREAT BRITAIN: 11♀, 14♂, Devon, Lustleigh, vii. 1934 (*R. C. L. Perkins*) (BMNH); 10 ♀, 10 ♂, Grampian 'Aberdeenshire', Ballater, Craigen Darroch, vii. 1975 (*Gauld*) (BMNH); 5 ♀, 7 ♂, Hampshire, New Forest, vii–viii. 1927–1936 (*Morley*) (BMNH); 40 ♀, 48 ♂, Staffordshire, Cannock Chase, bred ex *B. piniaria* on *Pinus sylvestris* L., vi. 1954 (*Forestry Commission*) (BMNH); 10 ♀, 10 ♂, same locality, on *Pinus* sp., viii. 1972–1973 (*Gauld*) (BMNH). NORWAY: 3 ♀, 3 ♂, Brekkesto, viii. 1938 (*Chaworth-Musters*) (BMNH). RUMANIA: 2 ♀, 1 ♂, no further data. SWEDEN: 1 ♀, Fjellfota sjö, vii. 1938 (*J. F. Perkins*) (BMNH). TURKEY: 1 ♀, Unye, vii. 1972, no further data (BMNH).

Heteropelma fulvitarse Cameron

(Text-figs 1, 2, 20, 28, 41, 52, 55, 62)

Heteropelma fulvitarse Cameron, 1899 : 111. Holotype ♀, INDIA (UM) [examined].
Heteropelma reticulatum Cameron, 1899 : 110. Holotype ♂, INDIA (UM) [examined]. **Syn. n.**
Anomalon binghami Cameron, 1907 : 14. Holotype ♂, INDIA: Sikkim (BMNH) [examined]. **Syn. n.**
Heteropelma fulvitarse Cameron; Morley, 1913*a* : 70.
[*Exochilum acheron* Morley, 1913*a* : 79. Partim, 1 ♂ from Shanghai. Misidentification.]
Anomalon binghami Cameron; Morley, 1913*a* : 84.
[*Heteropelma calcator* Wesmael; Morley, 1913*b* : 406. Misidentification.]
Heteropelma fulvitarsis Cameron; Morley, 1913*b* : 407.
Anomalon binghami Cameron; Morley, 1913*b* : 424.
Anomalon? binghami Cameron; Morley, 1914 : 325.
Heteropelma grossator Shestakov, 1923 : 46. Holotype ♀, U.S.S.R. (ZI) [examined]. **Syn. n.**
[*Heteropelma calcator* Wesmael; Dutt, 1923 : 18. Misidentification.]
Heteropelma grossator Shestakov; Meyer, 1935 : 60.
Heteropelma perlongum Cushman, 1937 : 297. Holotype ♀, TAIWAN (DEI) [examined]. **Syn. n.**
Heteropelma panargis Heinrich, 1953: 181. Holotype ♂, GERMANY (WEST) (HKT) [examined]. **Syn. n.**
Heteropelma perlongum Cushman; Uchida, 1958 : 94.
Heteropelma binghami (Cameron) Townes *et al.*, 1961 : 321.
Heteropelma fulvitarse Cameron; Townes *et al.*, 1961 : 321.
Heteropelma perlongum Cushman; Townes *et al.*, 1961 : 321.
Heteropelma reticulatum Cameron; Townes *et al.*, 1961 : 322.
Heteropelma grossator Shestakov; Townes *et al.*, 1965 : 383.

DESCRIPTION. Lower face 0·60–0·70 times as broad as high; clypeus apically simply convex, in profile rather flat; mandibles twisted about 20°, the upper tooth 2·0–3·0 times as long as lower. IOD 0·90–1·30 times as long as OOD; posterior ocellus separated from occipital carina by less than the greatest ocellar diameter. Head constricted posteriorly, vertex closely punctate to coriaceous; occipital carina evenly rounded or rarely medio-dorsally concave. Flagellum of moderate length, 50- to 55-segmented; 1st flagellar segment 2·10–2·50 times as long as 2nd; interantennal lamella strong, in profile quadrate. Face with long pale pubescence.

Pronotum coriaceous, anterior hook strong. Mesoscutum rather coarsely punctate, centrally rugose; notauli moderately strongly to weakly impressed, discernible to centre of scutum; mesoscutal pubescence short, usually ruddy or badious, rarely yellowish red. Mesopleuron dorsally rugose or reticulate, latero-ventrally finely punctate; epicnemial carina usually reaching

to centre of mesopleuron, bowed and with upper end reaching anterior pleural margin; sternaulus weak. Scutellum longitudinally concave or flat, elongate, rugosely punctate. Posterior transverse carina of mesosternum complete. Propodeum reticulate, without lateral protuberances, ventrally strongly sculptured; propodeum dorsally 0·80–0·95 times as long as broad.

Mid tibial spurs subequal, the outer about 1·1 times as long as inner. Hind leg with basitarsus 0·55–0·65 times as long as tibia, 3·60–4·20 times as long as 2nd tarsal segment; 2nd tarsal segment 1·70–2·60 times as long as 3rd segment; trochanter 0·75–0·95 times as long as trochantellus ventrally; hind tarsal claw geniculate, basally with a strong lamella. 2nd hind tarsal segment of ♂ ventrally impressed.

Wings weakly infumate; CI = 0·55–0·85; MI = 1·60–1·90; ICI = 0·70–1·30; NI = 0·40–0·50. Forewing length 10–15 mm.

Gaster with tergite 2 2·00–2·20 times as long as tergite 3; ♀ with ovipositor 0·50–0·60 times as long as tergite 2.

♂ genitalia. Distivolsella with spines arranged in an apical cluster and with short spines in a double row on ventral margin of distivolsella. Aedeagus in profile apically obliquely truncate; lateral sclerotized area apically acute, ventrally extended (Text-fig. 52).

Head black, face and genal marks yellow; antennae reddish or yellowish distally. Thorax black, tegulae reddish yellow. Anterior two pairs of legs yellowish, hind legs reddish, tibia distally darker, tarsi paler; gaster reddish.

Variation. This species was observed to be morphologically rather variable. There was observed to be a marked clinal variation in the specimens examined, those from the west of the range being generally darker and stouter than those from the east. Intermediates between the extremes of variation have been observed. To some extent the island populations, particularly that of Taiwan, are separable from the mainland form. The Taiwanese specimens were found to have the flagella pale yellowish and the scape not at all black marked as is most usual in this species. There are, however, no consistent morphological differences between the island and the mainland Chinese populations. As already mentioned there is a tendency for the specimens in the east of the range to be paler and so it is considered that the Taiwan population is conspecific with the mainland population.

A single ♀ from Hainan differs from the mainland Chinese population in having the lower tooth of the mandible subequal to the upper. There is quite a considerable variation of the ratio of lengths of the mandibular teeth within any one population and although no other specimens have been found with such subequal teeth it was considered possible that the Hainan specimen may represent an extreme variant of *H. fulvitarse*.

The holotypes of *H. grossator* Shestakov and *H. panargis* Heinrich were observed to have the head posteriorly strongly constricted and have a centrally depressed occipital carina. In all other features these species are similar to typical *H. fulvitarse* specimens and as head shape and the form of the occipital carina are very variable features *H. grossator* and *H. panargis* are included as synonyms of *H. fulvitarse*.

Isolated specimens of *H. fulvitarse* were observed to have the mid tibial spurs rather inequal, the longer about 1·50 times the length of the shorter. These specimens differ from *H. flaviscutellum* in having the interantennal lamella strongly developed, the 2nd hind tarsal segment of the ♂ with an impressed ventral area and having a black scutellum.

Remarks. This species apparently replaces *H. calcator* in the Oriental region. No biological information is at present available.

Host records. None available.

Distribution (Map 1). This species has been recorded from northern India and Sikkim (Cameron, 1899; 1907; Morley, 1913*b*). The latter author also recorded this species from Burma. It has been recorded from U.S.S.R. (Shestakov, 1923; Meyer, 1935) and Taiwan (Cushman, 1937; Uchida, 1958).

Material examined.

Heteropelma fulvitarse Cameron, holotype ♀, India: Assam, Khasia Hills (UM). *Heteropelma reticulatum* Cameron, holotype ♂, India: Assam, Khasia Hills (UM). *Anomalon binghami* Cameron, holotype ♂, India: Sikkim (BMNH). *Heteropelma grossator* Shestakov, holotype ♀, U.S.S.R.: Tomsk, Yelizavetinskiy (ZI). *Heteropelma perlongum* Cushman, holotype ♀, Taiwan (DEI). *Heteropelma panargis* Heinrich, holotype ♂, Germany (West): Steiermark (HKT); paratype, 1 ♂, same data as holotype (HKT).

Burma: 1 ♂, Maymayo, xii. 1937 (*Heinrich*) (HKT); 3♀, 5 ♂, Mt Victoria, iv. 1938 (*Heinrich*) (HKT). China: 6 ♀, Fukien, Shaowu Hsien, iv–v. 1942–1945 (*Maa*) (HKT); 1 ♀, Tibet, Yatung, vii. 1924 (*Hingston*) (BMNH); 1 ♀, no further data (BMNH). India: 2 ♀, Simla, vii. 1918 (*Brunetti*) (BMNH); 1 ♀, Assam, Mishmi Hills, xi. 1936 (BMNH); 2 ♂, no further data (BMNH); 3♀, 4♂, no further data (UM). Laos: 1 ♀, Muong Pek, xii. 1918 (*Salvaza*) (BMNH). Nepal: 1 ♀, 1 ♂, Taplejung, x–xi. 1961 (*Coe*) (BMNH). Taiwan: 1 ♀, Taiheizan, vii. 1934 (*Gressitt*) (HKT); 1 ♀, Musha, v. 1932 (*Gressitt*) (HKT); 1 ♂, Arizan, viii. 1908 (*Wileman*) (BMNH).

Heteropelma elongatum Uchida

(Text-figs 5, 22, 50)

Heteropelma calcator var. *elongatum* Uchida, 1928 : 238. Lectotype ♂, Japan (EIHU), designated by Townes *et al.*, 1965 : 383 [examined].
Heteropelma elongatum Uchida; Uchida, 1953 : 127.
Heteropelma elongatum Uchida; Uchida, 1958 : 94.
Heteropelma elongatum Uchida; Iwata, 1960 : 168.
Heteropelma elongatum Uchida; Townes *et al.*, 1965 : 383.

Description. Lower face 0·60–0·65 times as broad as high; clypeus apically simply convex, in profile rather flat; mandibles twisted about 15°, the upper tooth about 2·00 times as long as the lower. IOD 0·90–1·10 times as long as OOD; posterior ocellus separated from occipital carina by less than maximum ocellar diameter. Head constricted posteriorly, vertex coriaceous, laterally grading to coarsely punctate; occipital carina evenly rounded. Flagellum elongate, 61- to 65-segmented; 1st flagellar segment 2·20–2·30 times as long as 2nd; interantennal lamella of moderate size, in profile more or less triangular. Face with long pale pubescence.

Pronotum coriaceous, anterior hook strong. Mesoscutum centrally coriaceous, laterally punctate; notauli moderately strong, reaching beyond centre of scutum; mesoscutal pubescence short, yellowish red. Mesopleuron dorsally reticulate, latero-ventrally punctate; epicnemial carina strong, reaching to about centre of mesopleuron, usually with upper end remote from anterior pleural margin; sternaulus indistinct. Scutellum longitudinally concave. Posterior

transverse carina of mesosternum complete. Propodeum reticulate, without lateral protuberences, ventrally strongly sculptured; propodeum dorsally about 1·00 times as long as broad.

Mid tibial spurs subequal, the outer about 1·20 times as long as inner. Hind leg with basitarsus 0·66–0·68 times as long as tibia, 4·90–5·90 times as long as 2nd tarsal segment; 2nd tarsal segment 1·70–1·80 times as long as 3rd tarsal segment; trochanter 0·83–0·88 times as long as trochantellus ventrally; hind tarsal claw geniculate with a strong basal lamella. ♂ without an impressed area on 2nd hind tarsal segment.

Wings weakly infumate; Cl = 0·53–0·68; MI = 1·50–1·80; ICI = 0·60–1·20; NI = 0·50–0·65. Forewing length 12–17 mm.

Gaster with tergite 2 2·10–2·20 times as long as tergite 3; ♀ with ovipositor 0·45 times as long as tergite 2.

♂ genitalia. Distivolsella with spines arranged in apical cluster and with short row of double spines extending down ventral margin. Aedeagus in profile apically subequally bilobate; lateral sclerotized area apically broadened, indistinctly delineated.

Head black, lower face marks on genae yellow; antennae reddish. Thorax black, tegulae reddish yellow. Anterior two pairs of legs yellowish, hind legs reddish, tibia distally darker, trochanter ventrally pale. Gaster reddish.

Variation. Some variation in the coloration was observed. The female from China was found to have the hind coxa somewhat more swollen than is typical for this species. Slight variation in the shape of the interantennal lamella was also observed, a few specimens tending to have the lamella subquadrate in profile.

Remarks. This species is clearly very closely related to *H. fulvitarse* from which it differs in having a longer flagellum (61–65 segments compared with 50–55), the hind basitarsus extremely elongate (4·90–5·90 times as long as tarsus 2 compared with 3·60–4·20 times as long as tarsus 2) and having the 2nd hind tarsal segment of the ♂ devoid of an impressed area.

Host records. None available.

Distribution (Map 1). This species has previously been recorded from Japan (Uchida, 1928; 1958).

Material examined.

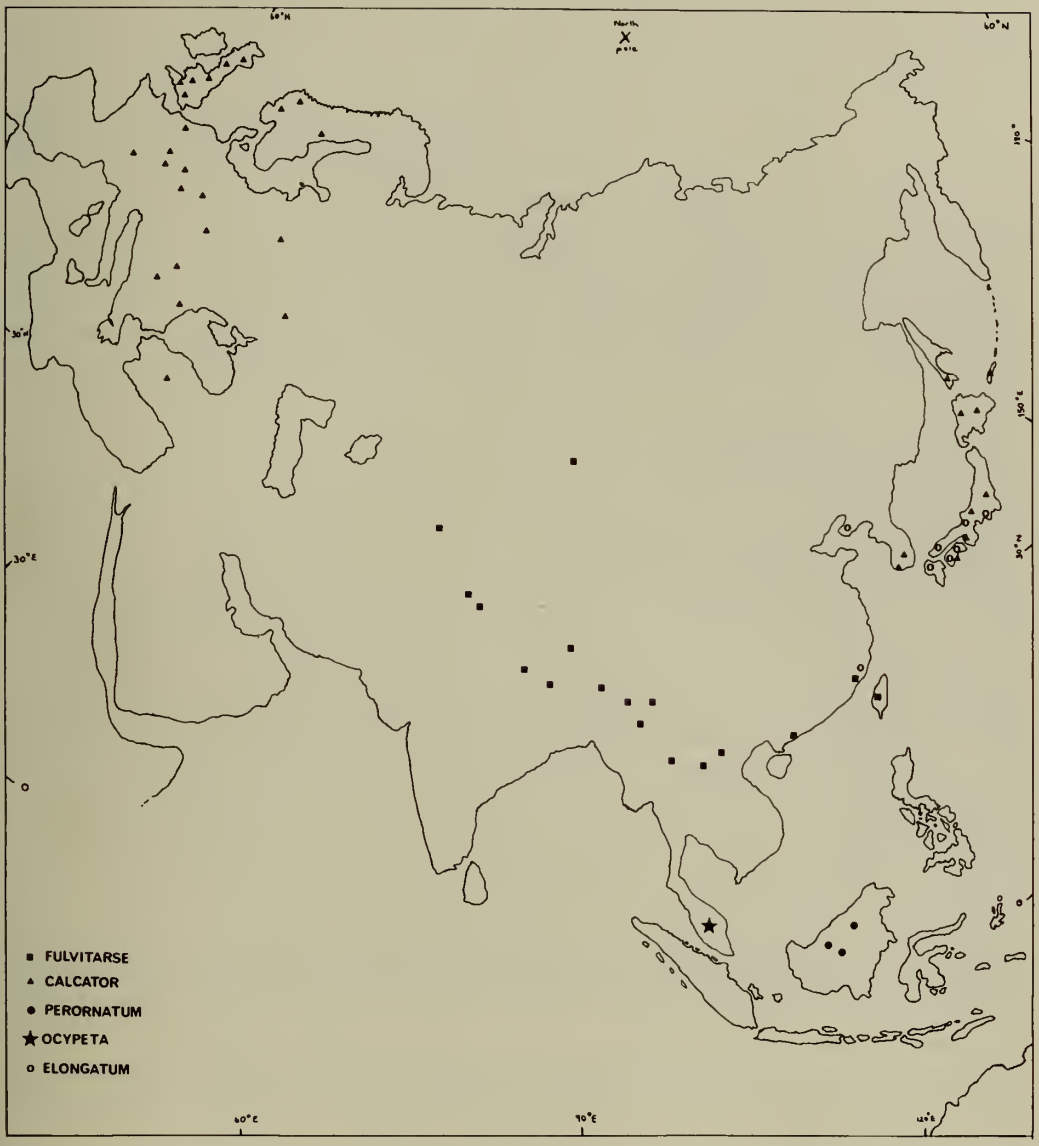
Heteropelma elongatum Uchida, lectotype ♂, Japan: Honshu, Tokyo, v. 1918 (*Teranischi*) (EIHU).

Japan: 1 ♂ (*Teranischi*) (HKT). China: 1 ♀, Fukien, Shaowu Hsien, ix. 1943 (*Maa*) (HKT); 2 ♂, same locality, v. 1943 (*Maa*) (HKT); 1 ♂, Tsin Leong San, vi. 1936 (*Kwantung*) (HKT).

Heteropelma flaviscutellum Uchida

(Text-figs 23, 38)

Heteropelma calcator var. *flaviscutellum* Uchida, 1928: 238. Lectotype ♂, Japan (EIHU), designated by Townes *et al.*, 1965 : 383 [examined].
Heteropelma tarsale Cushman, 1937 : 298. Holotype ♀, Taiwan (DEI) [examined]. **Syn. n.**
Heteropelma flaviscutellum Uchida; Uchida, 1958 : 95.
Heteropelma tarsale Cushman; Uchida, 1958 : 95.
Heteropelma tarsale Cushman; Townes *et al.*, 1961 : 322.
Heteropelma flaviscutellum Uchida; Townes *et al.*, 1965 : 383.



MAP 1. Palaearctic and Oriental zoogeographic regions (Zenithal equal projection; origin 40°N, 95°E) showing distributions of *Heteropelma fulvitarse*, *H. calcator*, *H. perornatum*, *H. ocypeta* and *H. elongatum*.

Description. Lower face 0·65–0·75 times as broad as high; clypeus apically simply convex, in profile swollen; mandibles twisted about 5°, upper tooth slightly less than 2·00 times as long as lower. IOD equal to OOD; posterior ocellus separated from occipital carina by about 0·90 times maximum ocellar diameter. Head posteriorly moderately constricted, vertex punctate; occipital carina medio-dorsally evenly rounded. Flagellum rather long and slender, 45-segmented, 1st flagellar segment about 1·80 times as long as 2nd; interantennal lamella almost absent. Face with long pallid pubescence.

Pronotum coriaceous, anterior hook moderately developed. Mesoscutum coarsely punctate; notauli strong, reaching beyond centre of scutum; mesoscutal pubescence short and pale. Mesopleuron dorsally coriaceous, ventrally sparsely punctate; epicnemial carina reaching above centre of pleuron, bowed so that upper end reaches anterior margin of mesopleuron, sternaulus weak. Scutellum convex, quadrate, striate. Posterior transverse carina of mesosternum complete. Propodeum reticulate, without lateral protuberance, ventrally strongly sculptured; propodeum dorsally 0·80 times as long as broad.

Mid tibial spurs inequal, the outer about 2·00 times as long as the inner. Hind leg with basitarsus 0·62–0·65 times as long as tibia, 4·30–6·10 times as long as 2nd tarsal segment; 2nd tarsal segment 1·30–1·90 times as long as 3rd tarsal segment; trochanter 0·73–0·77 times as long as trochantellus; hind tarsal claws as *fulvitarse*. Hind tarsus of ♂ without an impressed area.

Wings very weakly infumate; CI = 0·72–0·87; MI = 1·73–1·81; ICI = 1·44–1·60; NI = 0·63–0·70. Forewing length 10–11 mm.

Gaster with tergite 2 about 1·80 times as long as tergite 3; ♀ with ovipositor 0·50 times as long as tergite 2.

♂ genitalia. Not available for dissection.

Head black, lower face and vertical marks yellow; antennae reddish yellow. Thorax black, tegulae reddish, scutellum yellow. Anterior two pairs of legs yellow, hind legs brownish, coxae proximally darker, tibia distally dark brown, tarsi pale yellow.

Variation. The colour of this species is extremely variable. In some females the thorax was observed to be almost entirely badious with more reddish areas at bases of notauli, on mesopleuron and margins of the various sclerites. The scutellum, tegulae and sometimes subalar prominences were observed to be yellow. In the lighter specimens the antennae are yellowish, gaster except for the dorsum of tergite 2 orange-red, hind legs except for tarsi, distal 0·30 of tibia and dorsum of trochanter yellowish brown. Intermediates between this extreme and the typical form have been seen.

Remarks. The basitarsus and 2nd tarsal segment of males of this species are unusual in being particularly intimately associated and in outline continuous with each other. This feature enables males to be distinguished from all other species.

Host records. None available.

Distribution. Previously recorded from Japan and Taiwan (Uchida, 1928; 1958; Cushman, 1937).

Material examined.

Heteropelma flaviscutellum Uchida, lectotype ♂, Japan: Hokkaido, Jozankeim, viii. 1924 (*Uchida*) (EIHU). *Heteropelma tarsale* Cushman, holotype ♀, Taiwan: Kankau, Koshun, v. 1912 (*Sauter*) (DEI); paratypes, 1 ♀, same data as holotype, 1 ♂ same locality and collector as holotype, viii. 1908 (DEI).

Taiwan: 1 ♀, Kuraru, v. 1934 (*Gressitt*) (HKT).

Heteropelma perornatum (Cameron)

(Text-figs 6, 21, 24, 27, 44, 58)

Anomalon perornatum Cameron, 1902 : 50. LECTOTYPE ♀, Borneo: Sarawak (BMNH), here designated [examined].
Anomalon perornatum Cameron; Szépligeti, 1905 : 12.
Heteropelma perornatum (Cameron); Morley, 1913*a* : 70.
Heteropelma perornatum (Cameron); Townes *et al.*, 1961 : 321.

Description. Lower face 0·60–0·65 times as broad as high; clypeus apically simply convex, in profile weakly swollen; mandibles twisted about 35°, the upper tooth twice as long as the lower. IOD 1·10–1·40 times as long as OOD; posterior ocelli separated from occipital carina by about 0·90 times a maximum ocellar diameter. Head strongly constricted, vertex smooth with scattered punctures; occipital carina medio-dorsally usually dipped, rarely simply flattened. Flagellum of moderate length 53- to 55-segmented; 1st flagellar segment 1·90–2·10 times as long as 2nd; interantennal lamella weak, in profile obtusely triangular. Face with short pale pubescence.

Pronotum dorsally rather polished, smooth with obsolescent scattered punctures, ventrally strongly rugose, anterior hook strong. Mesoscutum punctate or rugulose; notauli weakly impressed but nevertheless obvious, extending beyond the centre of the scutum; mesoscutal pubescence short and pale. Mesopleuron dorsally strongly rugose, ventrally smooth with obsolescent punctures; epicnemial carina strong, reaching above centre of mesopleuron, bowed so that upper end reaches anterior pleural margin; sternaulus weak. Scutellum flat, elongate, rugosely striate. Posterior transverse carina of mesosternum very strongly raised, complete. Propodeum reticulate, without lateral protuberances, ventrally strongly sculptured; propodeum rather long, dorsally 0·90–1·10 times as long as broad.

Mid tibial spurs subequal, the outer about 1·10 times as long as the inner. Hind leg with basitarsus 0·65–0·70 times as long as tibia, 5·00–5·50 times as long as 2nd tarsal segment; 2nd tarsal segment 1·70–2·00 times as long as 3rd; trochanter 0·80–0·90 times as long as trochantellus ventrally; hind tarsal claw geniculate, strongly lobate. Hind tarsus 2 of male ventrally impressed on proximal 0·50 only.

Wings weakly infumate, CI = 0·75–0·95; MI = 1·65–1·75; ICI = 0·80–1·40; NI = 0·40–0·60. Forewing length 12–15 mm.

Gaster with tergite 2 2·00–2·20 times as long as tergite 3; ♀ with ovipositor 0·50–0·60 times as long as tergite 2.

♂ genitalia. Distivolsella with spines arranged in apical cluster and with short row of paired spines on ventral margin. Aedeagus in profile equally bilobate; lateral sclerotized area apically truncate, lower corner ventrally extended.

Head black, lower face and orbits yellow; flagellum black, rarely distally paler. Thorax black, tegulae reddish. Anterior two pairs of legs dark brown, tibia centrally and tarsi pale yellow. Gaster reddish brown.

Variation. Some variation in colour, especially that of the extent of the yellow on the hind tibia, has been observed.

Remarks. This species is morphologically closely related to *H. fulvitarse* which presumably it replaces in Borneo. Despite the close relationship the differences in pronotal sculpture and head shape will allow specific separation.

Host records. None available.

Distribution (Map 1). Recorded only from Borneo (Cameron, 1902; Szépligeti, 1905).

Material examined.

Anomalon perornatum Cameron, lectotype ♀, Borneo: Sarawak, Kuchung, vii. 1899 (BMNH); paralectotype 1 ♀, Borneo: xi. 1898 (*Shelford*) (BMNH).

Borneo: 1 ♀, Sarawak, Kuchung, vi. 1902 (BMNH); 3 ♀, 1 ♂, 'Borneo' x. 1850 (*Hewitt*) (RSM); 1 ♂, Kalimantan, Midden, viii. 1925 (*Siebers*) (HKT).

Heteropelma ocypeta sp. n.

(Text-figs 10, 35)

[*Heteropelma perornatum* (Cameron); Gauld, 1976 : 28. Misidentification.]

This and the following two new species, *H. celeno* and *H. aello*, are named after the Harpyai of classical mythology, in whom are embodied the concepts of wind spirits and predatory ghosts.

Description. Lower face 0·60–0·65 times as broad as high; clypeus apically simply convex, in profile flattened; mandibles twisted about 35°, the upper tooth about 2·50 times as long as the lower. IOD about 1·30 times OOD; posterior ocellus separated from occipital carina by 1·30–1·40 times maximum ocellar diameter. Head strongly constricted posteriorly, vertex coriaceous; occipital carina evenly rounded dorsally. Flagellum of moderate length, 49-segmented; 1st flagellar segment 2·10–2·40 times as long as 2nd; interantennal lamella weak, in profile obtusely triangular. Face with long badious or rufescent pubescence.

Pronotum dorsally punctate, lower 0·40 longitudinally striate, anterior hook strong. Mesoscutum centrally coriaceous, laterally punctate; notauli weakly impressed but nevertheless obvious, extending beyond centre of mesoscutum; mesoscutal pubescence long, badious. Mesopleuron dorsally coriaceous, latero-ventrally sparsely punctate; epicnemial carina reaching above centre of mesopleuron, bowed so that upper end reaches anterior pleural margin; sternaulus weak. Scutellum flat, subquadrate, punctate. Posterior transverse carina of mesosternum strong, complete. Propodeum reticulate, without lateral protuberances, ventrally strongly sculptured; propodeum dorsally 0·85–0·95 times as long as broad.

Mid tibial spurs extremely inequal, the outer of normal length, the inner vestigial. Hind leg with basitarsus about 0·60 times as long as tibia, 4·10–5·10 times as long as 2nd tarsal segment; 2nd tarsal segment 1·40–1·70 times as long as 3rd; trochanter 0·90–0·95 times as long as trochantellus ventrally; hind tarsal claw geniculate, basally strongly lobate.

♂ unknown.

Wings weakly infumate, CI = 0·95–1·00; MI = 1·63–1·69; ICI = 0·80–1·00; NI = 0·40–0·60. Forewing length 9–10 mm.

Gaster with tergite 2 2·40 times as long as tergite 3; ♀ with ovipositor 0·45–0·55 times as long as tergite 2.

Head black, lower face and orbits yellow; flagellum reddish, proximally black, distally yellow. Anterior two pairs of legs yellow; hind legs brownish yellow, coxae and distal 0·40 of hind tibia black. Gaster reddish yellow, indistinctly infuscate in irregularly defined areas.

Variation. The paratype was observed to be somewhat more hirsute than the holotype. Possibly some of the hair on this specimen has been removed in the past by cleaning.

Remarks. This species is similar in general morphology to *H. perornatum* but differs in having inequal mid tibial spurs, widely interspaced occipital carina and posterior ocelli, and having a more polished thorax.

Host records. None available.

DISTRIBUTION (Map 1). Malaysia.

MATERIAL EXAMINED.

Holotype ♀, MALAYSIA: Pahang, Cameron Highlands, 1700 m, xii. 1939 (*Pendlebury*) (BMNH).

Paratype. MALAYSIA: 1 ♀, Pahang, Cameron Highlands, 1600 m, vi. 1935 (*Pendlebury*) (BMNH).

Heteropelma celeno sp. n.

(Text-figs 11, 29, 32, 33, 47, 56, 57)

DESCRIPTION. Lower face 0·68–0·78 times as broad as high; clypeus apically simply convex, in profile more or less flat; mandibles twisted about 20°, the upper tooth about 2·00 times as long as lower. IOD 0·70–0·90 times as long as OOD; posterior ocellus separated from occipital carina by 0·90 times maximum ocellar diameter. Head strongly constricted, vertex closely but shallowly punctate; occipital carina dorsally flattened or slightly dipped. Flagellum of moderate length, 61- to 65-segmented; 1st flagellar segment 2·50–2·80 times as long as 2nd; interantennal lamella strong, in profile quadrate. Face with short pale pubescence.

Pronotum punctate to weakly coriaceous, anterior hook absent or vestigial. Mesoscutum coarsely and closely puncto-coriaceous, matt; notauli weak to indistinct; mesoscutal pubescence short, whitish. Mesopleuron dorsally alutaceous, latero-ventrally with fine even puncturation; epicnemial carina indistinct above lower corner of pronotum; sternaulus weak. Scutellum longitudinally concave, subquadrate, punctate. Posterior transverse carina of mesosternum complete, centrally weak. Propodeum reticulate with a pair of blunt lateral protuberances, ventrally weakly sculptured; propodeum dorsally 0·70–0·83 times as long as broad.

Mid tibial spurs subequal, the outer about 1·20 times as long as inner. Hind leg with basitarsus about 0·50 times as long as tibia, 2·40–2·80 times as long as 2nd tarsal segment; 2nd tarsal segment 1·70–2·10 times as long as 3rd; trochanter 0·70–0·90 times as long as trochantellus ventrally; hind tarsal claw abruptly curved, slender with a weak basal lobe. ♂ with 2nd hind tarsal segment strongly impressed ventrally.

Wings infumate, CI = 0·68; MI = 1·70–1·80; ICI = 0·30–0·90; NI = 0·20–0·30.

Gaster with tergite 2 about 2·50 times as long as tergite 3; ♀ with ovipositor 0·43–0·55 times as long as tergite 2.

♂ genitalia. Distivolsella with spines arranged in an apical cluster, some small spines distributed on clasping face. Aedeagus in profile apically very inequally bilobate; lateral sclerotized area apically simply acute.

Head, gaster and hind legs except for extreme distal end of basitarsus, tarsi 2–5 and coxae, black; lower face, orbits, extreme distal end of hind basitarsus and hind tarsi 2–5 white. Thorax, propodeum, anterior two pairs of legs and hind coxae reddish brown.

VARIATION. There was observed to be slight sexual dimorphism in this species. The males have the lower face immaculately white whereas that of the female has a pair of vertical black stripes extending from the anterior tentorial pits to the bases of the antennae. The hind tarsal claws of the males were observed to be slightly more slender than those of the females.

REMARKS. This and the following species, *H. aello*, are immediately distinguishable from other species of *Heteropelma* on account of their colour pattern. Unlike other species which are cryptically patterned these two species have bright warning coloration. This pattern is shared with three further synchronous and sympatric Papuan species, a species of *Aphanistes*, one of *Trichomma* and one of *Casinaria*

(all are believed to be undescribed). Whilst ichneumonoid mimics of Aculeata are not uncommon (*Metopius* species mimic Eumenid wasps and many species of Ichneumonidae mimic Pompilid wasps (Evans, 1968)), this mimicry complex apparently involves no aculeates. As *H. celeno* is the most numerous species in Malaise trap collections (and is thus arguably the commonest species) it is likely to be the model for the mimicry complex. It is probable therefore that this species is unpalatable to predators. It is difficult working with preserved material to ascertain why this species should be so unpalatable, but unlike most other species it was observed to have large slender claws, which were observed to be apically strongly curved and appeared to have a cavity in the distal part. A similar cavity has been observed by Townes (1940) in some Pimplinae, and he suggested that the claws may function as organs of defence.

Townes suggested that the readiness with which the live insects grasped a net with their claws might indicate that it is their habit, when attacked, to embed their claws in a prospective predator. Because the cavity structurally weakens the claw, the distal portion of it would break off remaining embedded in the prospective predator. Simultaneously the contents of the cavity (possibly a toxin) would be liberated. *Heteropelma celeno* may well have evolved a similar defence mechanism. In the material examined a large number of specimens were observed to have the claws incomplete, indicating that claw fractures readily occur.

This species is obviously closely related to *H. aello* but the relationship of these species to the remainder of the genus is not at all clear.

Host records. None available.

Distribution. New Guinea.

Material examined.

Holotype ♀, New Guinea: Wau & Mt Keinde, 2110 m, vi. 1969 (*Heinrich*) (HKT).

Paratypes. New Guinea: 3 ♀, 8 ♂, NE., Mt Kaindi, 2350 m, vi. 1971 (*Sedlacek & Samuelson*) (BPBM); 7 ♀, 5 ♂, NE., Mt Kaindi, 2350 m, ix. 1966 (*Samuelson*) (BPBM); 1 ♂, NE., Bulldog Road, 2405 m, v. 1969 (*Sedlacek*) (BPBM); 1 ♀, Papua, Dimifa, 2200 m, x. 1958 (*Gressitt*) (BPBM); 1 ♀, 1 ♂, Papua, Mt Hagen, 2000 m, vi. 1969 (*Heinrich*) (HKT).

Heteropelma aello sp. n.

(Text-figs 34, 53)

Description. Lower face 0·70–0·80 times as broad as high; clypeus apically simply convex, in profile weakly swollen; mandibles twisted about 40°, the upper tooth 2·50 times as long as lower. IOD 0·70–0·90 times as long as OOD; posterior ocellus separated from occipital carina by about 0·90 times maximum ocellar diameter. Head constricted, vertex with coarse scattered punctures; occipital carina medio-dorsally flattened. Flagellum of moderate length, 59- to 61-segmented; 1st flagellar segment 2·10–2·50 times as long as 2nd; interantennal lamella strong, in profile quadrate. Face with elongate black pubescence.

Pronotum coriaceous, anterior hook vestigial. Mesoscutum coarsely and very closely punctate, matt; notauli indistinct; mesoscutal pubescence short and dense, in ♀ badious, in ♂ testaceous. Mesopleuron dorsally coriaceous, latero-ventrally with fine even punctures;

epicnemial carina reaching about 0·40 of way up mesopleuron, its upper end widely separated from anterior pleural margin; sternaulus weak. Scutellum longitudinally concave, elongate, punctate. Posterior transverse carina of mesosternum broadly interrupted centrally. Propodeum reticulate with a pair of acute lateral protuberances, ventrally weakly sculptured; propodeum dorsally 0·56–0·66 times as long as broad.

Mid tibial spurs subequal, the outer about 1·20 times as long as the inner. Hind leg with basitarsus 0·50 times as long as tibia, 2·20–2·60 times as long as 2nd tarsal segment; 2nd tarsal segment 1·80–2·10 times as long as 3rd tarsal segment; trochanter 0·80–0·90 times as long as trochantellus ventrally; hind tarsal claw abruptly curved, unusually slender, with a small basal lobe. ♂ with 2nd hind tarsal segment ventrally strongly impressed.

Wings strongly infumate. CI = 0·80–0·90; MI = 1·50–1·75; ICI = 0·90–1·10; NI = 0·45–0·55. Forewing length 13–16 mm.

Gaster with tergite 2 2·30 times as long as tergite 3; ♀ with ovipositor 0·67 times as long as tergite 2.

♂ genitalia. Aedeagus in profile subequally bilobate; lateral sclerotized area apically simply acute.

Head, gaster, hind femora and basitarsi except distally, also usually ill defined areas on mesoscutum, pronotum and mesosternum blackish; face centrally usually, distal apex of hind basitarsus and hind tarsi 2–5 stramineous; thorax, propodeum, anterior two pairs of legs and hind coxae and trochanteral segments reddish brown.

VARIATION. The areas of black colour on the thorax were observed to be variable in their extent.

REMARKS. This species is apparently closely related to *H. celeno* from which it may be distinguished not only in the characters mentioned in the key but also in having a more strongly developed epicnemial carina, more strongly twisted mandibles and having the NI larger.

HOST RECORDS. None available.

MATERIAL EXAMINED.

Holotype ♀, NEW GUINEA: SE., Iongai, 1700–1900 m, 9.xi.1965 (*Sedlacek*) (BPBM).

Paratypes. NEW GUINEA: 1 ♂, NE., Lake Siruki, 2800–2900 m, 15.vi.1963 (*Sedlacek*) (BPBM); 1 ♂, SE., Mt Giluwe, 2500–3300 m, 2.vi.1963 (*Sedlacek*) (BPBM).

Heteropelma scaposum (Morley)

(Text-figs 30, 37, 49, 60, 64)

Exochilum scaposum Morley, 1913*a* : 75. Lectotype ♀, AUSTRALIA (BMNH), selected by Morley, designated by Townes *et al.*, 1961 : 322 [examined].

Exochilum atrichiosoma Morley, 1913*a* : 77. Lectotype ♀, AUSTRALIA (BMNH), selected by Morley, designated by Townes *et al.*, 1961 : 320 [examined]. [Synonymized by Gauld, 1974 : 543.]

Exochilum scaposum Morley; Turner, 1919 : 555.

Exochilum atrichiosoma Morley; Turner, 1919 : 555.

Heteropelma atrichiosoma (Morley) Townes *et al.*, 1961 : 320.

Heteropelma scaposum (Morley) Townes *et al.*, 1961 : 322.

Heteropelma scaposum (Morley); Gauld, 1974 : 543.

DESCRIPTION. Lower face 0·75–0·85 times as broad as high; clypeus apically almost truncate, in profile flat; mandibles not twisted, the upper tooth about 2·00 times as long as the lower;

IOD 1·20–1·40 times as long as OOD; posterior ocellus separated from occipital carina by about 1·20 times maximum ocellar diameter. Head not posteriorly constricted, vertex with deep scattered punctures; occipital carina mediodorsally flat or dipped. Flagellum moderately long, 48- to 58-segmented, 1st flagellar segment 2·20–2·60 times as long as 2nd; interantennal lamella strong, in profile quadrate. Face with pubescence short to long, always pale.

Propodeum punctate, anterior hook moderately well developed. Mesoscutum usually punctate; notauli weak but reaching beyond the centre of the scutum; mesoscutal pubescence usually short and pale. Mesopleuron dorsally rugose, latero-ventrally punctate; epicnemial carina reaching above centre of mesopleuron, bowed and with upper end close to anterior pleural margin; sternaulus moderately impressed, broad. Scutellum slightly convex in longitudinal profile, usually with a shallow concavity posteriorly, subquadrate, punctate. Posterior transverse carina of mesosternum complete, rarely rather weak centrally. Propodeum reticulate without lateral protuberances, ventrally sculptured; propodeum dorsally 0·70–0·90 times as long as broad.

Mid tibial spurs almost equal in length. Hind leg with basitarsus 0·50–0·60 times as long as tibia, 2·30–2·50 times as long as 2nd tarsal segment; 2nd tarsal segment 2·20–2·80 times as long as 3rd; trochanter 0·80–0·90 times as long as trochantellus ventrally; hind tarsal claws geniculate, basally lobate. ♂ with 2nd hind tarsal segment impressed ventrally.

Wings very weakly infumate. CI = 0·70–0·90; MI = 1·55–1·65; ICI = 0·85–1·20; NI = 0·50–0·60. Forewing length 6–15 mm.

Gaster with tergite 2 1·80–1·90 times as long as tergite 3; tergite 3 0·90 times or more (usually more than 1·00 times) as long as tergite 4; ♀ with ovipositor about 0·60 times as long as tergite 2.

♂ genitalia. Distivolsella with spines scattered on clasping face. Aedeagus in profile apically somewhat obliquely truncate; lateral sclerotized area broad, apically indistinctly defined.

Head blackish; lower face and orbital marks yellow; antennae black to reddish, scape ventrally yellow. Thorax black, tegulae yellow. Anterior two pairs of legs yellow; hind legs red-brown, with dorsum of trochanter, trochantellus, distal apex of tibia and proximal end of basitarsus black; segments 2–4 and distal part of basitarsus yellow. Gaster reddish with dorsum of tergite 2 infuscate.

Variation. This species was observed to have one of the largest size ranges of any *Heteropelma* species. Smaller specimens were observed to have smaller values of CI than larger specimens. Larger specimens were also disproportionately more hairy, especially on the thorax. The shape of the head was observed to be rather variable. Examination of a long series of specimens from a number of localities has shown that specimens from coastal regions of the southern half of Australia are generally larger and with darker antennae than are those from Queensland. The type-material of *H. atrichiosoma* is merely a less yellow marked form of *H. scaposum*. A number of intermediates have been seen thus confirming the opinion that the former species is synonymous with the latter.

Remarks. The basally dark basitarsus distinguishes the Australian species of *Heteropelma* from all others except the South American species. *H. scaposum* is closely related morphologically to *H. perniciosum* and *H. flavitarse*. It is distinct from the latter in having the hind tarsal claws geniculate and basally strongly lobate as well as being less hirsute and less extensively dark marked. It differs from *H. perniciosum* less markedly, indeed the only reliable features permitting separation are the relative lengths of the 3rd and 4th gastral tergites and the coloration. Whether these differences will remain when more material is available is yet to be ascertained.

H. scaposum is the commonest Australian Anomalonid and as a common parasite of *Heliothis armigera* may be an insect of considerable economic importance. As yet no worker has investigated the biology of this species.

It has been possible to examine the cephalic capsule of the final instar larva of this species. It was found to be similar to that of *H. calcator* except that the hypostoma was straighter and the labial sclerite more complete ventrally (Text-figs 36, 37).

Host records. Girault (1925) recorded this species as a parasite of *Heliothis armigera* (Hübner). Specimens forwarded to the Commonwealth Institute of Entomology for identification are from:

Heliothis zea (Boddie) (=*obsoleta* F.) (*Ballard*, xii. 1925)

Heliothis armigera (Hübner) (Department of Agriculture, New South Wales, vi. 1974)

Omphaloides australasiae (F.) (*Williams*, vi. 1973).

Distribution. Australia.

Material examined.

Exochilum scaposum Morley, lectotype ♀, Australia: Queensland, Mackay (*Turner*) (BMNH); paralectotypes, 2 ♀, 4 ♂, same data as lectotype (BMNH). [In previous work (Gauld, 1974) only one ♀ paralectotype was mentioned; subsequently a further ♀ which must also be considered to be a paralectotype was discovered in the accessions of the BMNH. Morley failed to state the number of specimens upon which his description was based so that other paralectotypes may also exist.] *Exochilum atrichiosoma* Morley, lectotype ♀, Australia: Victoria (*du Boulay*) (BMNH); paralectotypes 2 ♀, same data as lectotype (BMNH); 1 ♀ 'Western Australia'. [This specimen which bears no additional data, was labelled as 'co-type' by Morley. It is presumably the specimen or one of the specimens from Champion Bay, Western Australia, to which Morley refers. The specimens collected by French in 1901, which are also paralectotypes, have not been located.]

In addition to material listed by Gauld (1974) the following specimens have been examined: Australia: 1 ♀, 4 ♂, Queensland, Biggenden (*H. Frauca*) (ANIC); 4 ♀, 3 ♂, Q., Brisbane, 1911–1913 (*H. Hacker*) (QM); 4 ♀, Q., 50 km west of Brisbane, ii. 1961 (*Gressitt*) (BPBM); 1 ♀, Q., Gatton, xii. 1925 (*Ballard*) (BMNH); 1 ♀, Q., Halifax, vi. 1919 (*B. Williams*) (BPBM); 4 ♂, Q., Mt Glorius (*Straatman*) (ANIC); 2 ♀, 1 ♂, Q., Mt Glorius, ii. 1961 (*Gressitt*) (BPBM); 1 ♂, Q., Mt Glorius, i. 1963 (*Brooks*) (BPBM); 1 ♂, New South Wales, Beechcroft, vi. 1973 (*Williams*) (BMNH); 1 ♂, Western Australia, Bejoording, ix. 1950 (*McMillan*) (WAM); 1 ♂, W.A., Carnac Is., ix. 1934 (*Norris*) (HKT); 2 ♀, 7 ♂, W.A., Coorow, 1952 (*McIntosh & Calaby*) (ANIC); 2 ♀, W.A., Cottesloe, ix. 1948 (*Glauret*) (WAM); 1 ♂, W.A., Cottesloe, xi. 1945 (*Glauret*) (WAM); 1 ♂, W.A., Dumbleyung, x. 1963 (*Udell*) (WAM); 5 ♀, 4 ♂, W.A., Merredin, x. 1952 (*Douglas*) (WAM); 2 ♀, 1 ♂, W.A., Mogamber, x. 1938 (*A. Turner*) (QM); 1 ♀, W.A., Nedlands, ix. 1963 (*Fuller*) (WAM); 2 ♀, W.A., Northam, xi. 1963 (*Sedlacek*) (BPBM); 1 ♀, W.A., Nukarni, ix. 1948 (*Willis*) (WAM); 1 ♀, 6 ♂, W.A., Rottnest Is., 1936/7 (*Glauret*) (WAM); 2 ♀, W.A., Yallingup, xi. 1942 (*Glauret*) (WAM); 2 ♀, Tasmania, Hobart, i. 1934 (*A. Turner*) (QM); 1 ♀, T., Launceston, ii. 1916 (*Littler*) (QM).

Heteropelma flavitarse (Brullé)

(Text-fig. 31)

Anomalon flavitarse Brullé, 1846 : 171. Holotype ♂, AUSTRALIA (lost).
Anomalon trichiosomum Cameron, 1906 : 182. Holotype ♀, AUSTRALIA (BMNH). [Synonymized by Gauld, 1974 : 542.]
Exochilum trichiosoma (Cameron) Morley, 1913*a* : 77.
Barylypa flavitarsis (Brullé) Morley, 1913*a* : 81.
Heteropelma? flavitarse (Brullé) Townes *et al.*, 1961 : 321.
Heteropelma trichiosomum (Cameron) Townes *et al.*, 1961 : 322.
Heteropelma flavitarse (Brullé) Gauld, 1974 : 542.

DESCRIPTION. Lower face 0·70–0·80 times as broad as high; clypeus subtruncate apically, in profile flat; mandibles not twisted, upper tooth about 2·50 times as long as lower; IOD 1·20–1·30 times OOD; posterior ocellus separated from occipital carina by a distance about equal to the maximum ocellar diameter. Head not posteriorly constricted, vertex punctate; occipital carina mediodorsally flattened. Flagellum of moderate length, stout, 60- to 65-segmented; 1st flagellar segment 2·80–3·00 times as long as 2nd; interantennal lamella strong, in profile almost quadrate. Face with long badious pubescence.

Pronotum punctate, anterior hook weak. Mesoscutum punctate; notauli weak, reaching to centre of scutum but not discernible at anterior extremities; mesoscutal pubescence blackish. Mesopleuron dorsally coriaceous, ventrolaterally coarsely punctate; epicnemial carina not reaching above lower 0·4 of mesopleuron, its upper end not close to anterior pleural margin; sternaulus moderately strong. Scutellum moderately convex, subquadrate, rugosely punctate. Posterior transverse carina of mesosternum complete. Propodeum finely reticulate, without lateral projections, ventrally sculptured; propodeum dorsally 0·70–0·80 times as long as broad.

Mid tibial spurs equal. Hind leg with basitarsus 0·50–0·60 times as long as tibia, 2·50–2·80 times as long as 2nd tarsal segment; 2nd tarsal segment 2·20–2·30 times as long as 3rd; trochanter about 0·80 times as long as trochantellus ventrally; hind tarsal claws simply curved with a weak basal lamella. Male with 2nd hind tarsal segment ventrally impressed.

Wings moderately infumate; CI = 0·80–0·85; MI = 1·50–1·60; 1CI = 1·00–1·20; NI = 0·40–0·50. Forewing length 13–16 mm.

Gaster with tergite 2 1·90–2·00 times as long as tergite 3; tergite 3 about 1·10 times as long as tergite 4. ♀ with ovipositor 0·60–0·65 times as long as tergite 2. ♂ genitalia similar to those of *H. scaposum*.

Head black, lower face centrally (rarely entirely) and small mark on vertex yellow; flagellum black, scape indistinctly red ventrally. Thorax black, tegulae red. Legs red-brown, forelegs paler; hind tibiae, except proximally, and hind basitarsus proximally black; hind tarsi 2–4 yellowish. Gaster dark red, dorsally and ventrally infuscate.

VARIATION. Some variation in the facial colour was observed. The black areas are typically present as a pair of stripes extending from tentorial pits to antennal bases, but these stripes vary in width until in extreme cases the entire lower face is black except for a small central yellow mark. In other cases the width of the stripes is reduced and in isolated specimens the stripes were not discernible except as small infuscate areas above the anterior tentorial pits and below the antennal bases. Males were generally observed to have the face less black marked than females.

REMARKS. The tarsal claws, ratio of hind tarsal lengths, clypeal structure and head shape would seem to indicate that this species is one of the least specialized species of *Heteropelma*. This observation is discussed further below (p. 206). This species is probably closely related to the other Australian species.

HOST RECORDS. None known.

DISTRIBUTION (Map 2). This species is apparently restricted to the southern part of Australia and Tasmania.

MATERIAL EXAMINED.

Anomalon trichiosomum Cameron, holotype ♀, AUSTRALIA: no further data (BMNH).

In addition to the material listed by Gauld (1974) the following specimens have been examined: AUSTRALIA: 1 ♀, Tasmania, Eaglehawk Neck, ii. 1913 (*R. E. Turner*) (HKT); 2 ♂, Western Australia, Guildford, viii. 1962 (*McMillan*) (WAM); 1 ♂, W.A., Kings Park, iv. 1974 (*Postmus & Wade*) (WAM); 1 ♀, W.A., Norrogin, x. 1936 (*Douglas*) (WAM); 1 ♀, W.A., Yallingup, x. 1913 (*R. E. Turner*) (BMNH).

Heteropelma perniciosum (Turner)

Exochilum perniciosum Turner, 1919 : 554. Lectotype ♀, AUSTRALIA (BMNH), designated by Gauld, 1974 : 544 [examined].
Heteropelma perniciosum (Turner) Townes *et al.*, 1961 : 321.
Heteropelma perniciosum (Turner); Gauld, 1974 : 544.

DESCRIPTION. Lower face 0·60–0·65 times as broad as high; clypeus apically simply convex, in profile slightly swollen; mandibles not twisted, upper tooth about 1·80 times as long as lower. IOD 1·20–1·30 times as long as OOD; posterior ocellus separated from occipital carina by about 1·20 times ocellar diameter. Head weakly constricted posteriorly, vertex sparsely but deeply punctate; occipital carina mediodorsally evenly rounded. Flagellum moderately long, 45- to 48-segmented; 1st flagellar segment about 2·00 times as long as 2nd; interantennal lamella strong, in profile quadrate. Face with long sparse pubescence.

Pronotum coriaceous, anterior hook strong. Mesoscutum coarsely punctate; notauli weak but discernible beyond centre of mesoscutum; mesoscutal pubescence short and pale. Mesopleuron coriaceous, latero-ventrally closely punctate; epicnemial carina reaching to centre of pleuron, bowed so that upper end approaches anterior pleural margin; sternaulus weak. Scutellum longitudinally concave, elongate, coarsely puncto-striate. Posterior transverse carina of mesosternum complete. Propodeum reticulate, without lateral projections, ventrally sculptured; propodeum dorsally about 0·80 times as long as broad.

Mid tibial spurs equal. Hind leg with basitarsus about 0·55 times as long as tibia, 2·10–2·20 times as long as 2nd tarsal segment; 2nd tarsal segment 2·40 times as long as 3rd; trochanter 0·80 times as long as trochantellus ventrally; hind tarsal claws geniculate, with strong basal lamella. Male unknown.

Wings very weakly infumate; CI = 0·80–0·85; MI = 1·50–1·60; ICI = 1·10–1·20; NI = 0·50. Forewing length 8–9 mm.

Gaster with tergite 2 about 2·40 times as long as tergite 3; tergite 3 0·70–0·80 times as long as tergite 4. ♀ with ovipositor about 0·60 times as long as tergite 2.

Head black, lower face, marks on vertex and genae reddish; antennae red, proximally darker. Thorax reddish brown, mesoscutum and mesosternum black marked. Legs red, hind tibia distally and basitarsus proximally black. Gaster unicolorous red.

REMARKS. The validity of this species must remain questionable for several reasons. Firstly, the two females are very similar to *H. scaposum*, differing only in colour and relative lengths of tergites 3 and 4. Secondly, although extensive collections of Australian specimens have been examined, no further examples of this species have been seen. However, as the fauna of Western Australia is as yet

only poorly collected it is conceivable that this species has been overlooked by all collectors since Turner. In the present work, therefore, *H. perniciosum* is provisionally retained as a distinct species.

Host records. None available.

Distribution. Australia (Western Australia only).

Material examined.

Exochilum perniciosum Turner, lectotype ♀, Australia: Western Australia, Yallingup (*Turner*) (BMNH); paralectotype 1 ♀, same data as lectotype (BMNH).

Heteropelma quodi (Vachal)

(Text-figs 7, 45)

Anomalon quodi Vachal, 1907 : 120. Holotype ♂, New Caledonia (?MNHN).
Heteropelma quodi (Vachal) Townes *et al.*, 1961 : 321.

The Vachal types are all believed to be in the MNHN, Paris. Mme Kelner-Pillault was so kind as to search for the holotype of *H. quodi* and, although she located the type-material of other species described by Vachal in the same publication, she was unable to locate that of *H. quodi*. I have before me a pair of specimens of this distinct species, the male of which agrees exactly with the description given by Vachal (1907). The descriptions below are based on these specimens.

Description. Lower face 0·62–0·66 times as broad as high; clypeus apically simply convex, in profile almost flat; mandibles twisted about 40°, the upper tooth about 3·00 times as long as the lower. IOD 1·30–1·50 times as long as OOD; posterior ocellus separated from occipital carina by a distance about equal to an ocellar diameter. Head constricted, vertex coarsely but not closely punctate; occipital carina medio-dorsally weakly flattened. Flagellum of moderate length, 51- to 53-segmented; 1st flagellar segment 1·90–2·10 times as long as 2nd; interantennal lamella strong, in profile quadrate. Face with moderately long pale pubescence.

Pronotum strongly punctate, anterior hook moderately developed. Mesoscutum coarsely punctate, subpolished; notauli strongly impressed, reaching beyond centre of scutum; mesoscutal pubescence short, badious. Mesopleuron dorsally rugose, latero-ventrally with numerous finely regularly interspaced punctures; epicnemial carina strong, its upper end not reaching to centre of pleuron and separated from anterior pleural margin; sternaulus weak. Scutellum weakly convex, somewhat elongate, coarsely punctostriate. Posterior transverse carina of mesosternum complete. Propodeum reticulate, without lateral protuberances, ventrally strongly carinate; propodeum dorsally 0·80 times as long as broad.

Mid tibial spurs subequal, the outer about 1·20 times as long as the inner. Hind leg with basitarsus 0·50 times as long as tibia, 2·20–2·50 times as long as 2nd tarsal segment; 2nd tarsal segment 1·80–2·30 times as long as 3rd tarsal segment; trochanter ventrally 0·70 times as long as trochantellus; hind tarsal claw geniculate, with moderately developed basal lobe. ♂ with 2nd hind tarsal segment ventrally impressed.

Wings blackish; CI = 0·80–0·90; MI = 1·45–1·65; ICI = 1·20–4·00; NI = 0·55–0·65. Forewing length 9–10 mm.

Gaster with tergite 2 about 2·10 times as long as tergite 3; ♀ with ovipositor 0·60 times as long as tergite 2.

♂ genitalia. Distivolsella with spines arranged in apical cluster and with a short row of double spines on ventral margin. Aedeagus in profile apically subequally bilobate; lateral sclerotized area apically indistinctly defined.

Insect predominantly black, lower face, marks on genal orbits, anterior two pairs of legs (except for the coxae partially) and hind tarsi (except basitarsus proximally) yellow.

VARIATION. The ♀ was observed to have the fore coxae darker than the ♂.

REMARKS. The form of the hind legs and head shape indicate that this species is closely related to the Australian species. It is quite distinct from the Papuan species-group in having a simple propodeum and an obvious pronotal hook. Gupta (1962) found in the Ichneumonid genus *Theronia* a close relationship between Australian and New Caledonian species and a similar relationship has been observed in species of the genus *Agrypon* (Gauld, unpublished data). This data would seem to indicate that although New Caledonia is often placed in the Papuan zoogeographic region at least part of its fauna has been derived, possibly through chance migration, from mainland Australia and not from New Guinea via the Solomon Archipelago.

HOST RECORDS. None available.

DISTRIBUTION. New Caledonia.

MATERIAL EXAMINED.

NEW CALEDONIA: 1 ♀, Foret de Thi, ii. 1957 (*Rageau*) (BMNH); 1 ♂, Mt Koghi, x. 1967 (*Sedlacek*) (BPBM); 1 ♂, Bourail, xii. 1930 (*Cheesman*) (BMNH).

Heteropelma savaiiense (Fullaway)

(Text-figs 9, 25, 39)

Therion savaiiense Fullaway, 1940 : 400. Holotype ♂, SAMOAN ISLANDS (BPBM) [examined].
Heteropelma savaiiense (Fullaway) Townes *et al.*, 1961 : 322.

DESCRIPTION. Lower face 0·63 times as broad as high; clypeus apically simply convex, in profile weakly swollen; mandibles twisted about 35°, the upper tooth more than 2·00 times as long as the lower. IOD 1·10 times as long as OOD; posterior ocellus separated from occipital carina by 1·10 times maximum ocellar diameter. Head somewhat constricted, vertex coarsely punctate; occipital carina dorsally slightly flattened. Flagellum incomplete, 1st flagellar segment 1·90 times as long as 2nd; interantennal lamella weak, in profile obtusely triangular. Face with short sparse pubescence.

Pronotum granulate, anterior hook weak. Mesoscutum very coarsely rugose, matt; notauli strongly impressed, reaching to centre of scutum; mesoscutal pubescence short, white. Mesopleuron dorsally rugose, latero-ventrally sparsely punctate; epicnemial carina strong, close to anterior margin of pleuron, its upper end reaching pleural margin slightly above the centre of the mesopleuron; sternaulus strongly impressed. Scutellum weakly convex, subquadrate, punctostriate. Posterior transverse carina of mesosternum complete, centrally somewhat faint. Propodeum reticulate, without lateral projections, ventrally with strong carinae; propodeum dorsally 0·80 times as long as broad.

Mid tibial spurs subequal, the outer 1·30 times as long as the inner. Hind leg with basitarsus 0·50 times as long as tibia, 2·40 times as long as 2nd tarsal segment; 2nd tarsal segment 1·90 times as long as 3rd segment; trochanter 0·90 times as long as trochantellus ventrally; hind tarsal claw geniculate, with weak basal lobe; tarsus 2 ventrally impressed.

Wings hyaline: CI = 0·85; MI = 1·95; ICI = 0·25; NI = 0·26. Forewing length 7·5 mm.

Gaster with tergite 2 1·60 times as long as tergite 3.

♀ unknown.

♂ genitalia. Not available for dissection.

Insect entirely orange-red except for the lower face, genae and anterior two pairs of legs, which are yellowish, and the frons and vertex, which are brown.

Remarks. This species is probably closely related to *H. quodi*. Very little collection of Ichneumonidae has been undertaken in the islands east of New Guinea. *Heteropelma* species have been found on two groups, New Caledonia and Samoa. It is possible that a number of other species await discovery in this general area.

Host records. None available.

Distribution. Samoan Islands.

Material examined.

Holotype ♂, Samoan Islands: Savaii, Safune, 650–1300 m, rain forest, v. 1924 (*E. Bryan*) (BPBM).

Heteropelma townesi sp. n.

(Text-figs 8, 40, 43, 51)

This species is named after Dr H. K. Townes who was kind enough to inform the author of the existence of this Neotropical species.

Description. Lower face 0·60–0·70 times as broad as high; clypeus apically rather flatly convex, in profile weakly swollen; mandibles twisted about 40°, the upper tooth about 3·00 times as long as the lower. IOD about 1·00 times as long as OOD; posterior ocellus separated from occipital carina by about 1·10 times maximum ocellar diameter. Head constricted, vertex with scattered punctures, medio-dorsally rugose; occipital carina incomplete medio-dorsally. Flagellum of moderate length, 45- to 47-segmented; 1st flagellar segment 1·90–2·50 times as long as 2nd; interantennal lamella moderately strong, in profile more or less triangular. Face with short pale pubescence.

Pronotum polished with very fine scattered punctures and with strongly impressed margins; anterior hook moderately developed. Mesoscutum polished, evenly punctate, punctures separated by their own diameters; notauli distinct, nearly reaching to posterior margin of mesoscutum; mesoscutal pubescence short, pale. Mesopleuron dorsally longitudinally striate, latero-ventrally finely punctate; epicnemial carina reaching to centre of mesopleuron, bowed so that upper end reaches anterior pleural margin; sternaulus weak. Scutellum longitudinally concave, subquadrate, punctate. Posterior transverse carina of mesosternum complete. Propodeum reticulate, without lateral protuberances; propodeum dorsally 0·70–0·75 times as long as broad.

Mid tibia unicalcarate. Hind leg with basitarsus 0·50–0·60 times as long as tibia, 1·80–3·80 times as long as 2nd tarsal segment; 2nd tarsal segment 2·10–3·50 times as long as 3rd segment; trochanter 1·00–1·05 times as long as trochantellus ventrally; hind tarsal claw strongly geniculate, basally lobate; ♂ with hind tarsus 2 with a groove-like ventral impression.

Wings infumate; CI = 0·40–0·55; MI = 2·10–2·40; ICI = 0·70–1·10; NI = 0·70–0·90. Forewing length 10–14 mm.

Gaster with tergite 2 about 2·30 times as long as tergite 3; ♀ with ovipositor 0·50–0·60 times as long as tergite 2.

♂ genitalia. Aedeagus in profile with dorsal lobe strongly reduced; lateral sclerotized region narrow, apically rounded.

Insect almost entirely black, yellow marked on lower face, genae, fore legs (except tarsi distally), mid legs (except coxae proximally, distal 0·50 of femur, tibia on proximal 0·10 and distal 0·40 and tarsi 2–4), ventral surface of hind trochantellus and band on proximal third of hind tibia; gaster indistinctly reddish brown in part.

VARIATION. There was observed to be an unusual degree of variation in the ratio of the first two hind tarsal segments of this species. One of the females examined, and subsequently not included as a paratype, was observed to be smaller than the holotype and have a red marked gaster. This specimen is also unusual in having a transverse impression dorsally on each hind femur. Whether this is a teratological aberration, or within the normal range of variation for this species is not known. It is possible that this specimen may represent a second and undescribed Neotropical species.

REMARKS. This species is morphologically quite distinct in having the mid tibia unicalcarate, occipital carina incomplete, trochanters equal to or longer than the trochantelli, etc. However, when compared with the Therionini as a whole it is obvious from the form of the clypeus, form of the hind tarsi, structure of the ovipositor and shape of the claws that this species is an aberrant species of *Heteropelma* and does not warrant further taxonomic distinction. The affinities of this species are not clear but the structure of the legs and clypeus would seem to indicate that this species may be allied to the *H. calcator* species-group. Alternatively it is possible that this species may be closer to some of the Australasian species and have developed the elongate tarsi quite separately from the *calcator*-group. Whatever its ancestry, this species has obviously been separated from the main group of species for a considerable period. This species is not at all closely related to the Nearctic species.

HOST RECORDS. None available.

DISTRIBUTION (Map 2). Brazil.

MATERIAL EXAMINED.

Holotype ♀, BRAZIL: Nova Teutonia, Santa Catarina, xi. 1970 (*Plaumann*) (HKT).

Paratypes. 1 ♂, BRAZIL: Nova Teutonia, Santa Catarina, xi. 1968 (*Plaumann*) (HKT); 1 ♂, Nova Teutonia, xii. 1938 (*Plaumann*) (BMNH).

Material excluded from type-series. BRAZIL: 1 ♀, Nova Teutonia, Santa Catarina, xi. 1970 (*Plaumann*) (HKT).

Heteropelma datanae Riley

(Text-figs 26, 54)

Anomalon flavicorne Brullé, 1846 : 171. Holotype ♀, U.S.A.: Philadelphia (?MNHN). Junior primary homonym of *Anomalon flavicorne* Say, 1823.

Heteropelma flavicorne (Brullé) Norton, 1863 : 360.

Heteropelma datanae Riley, 1888 : 177. LECTOTYPE ♀, U.S.A. (USNM), by present designation [examined].

Heteropelma flavicorne (Brullé); Ashmead, 1900 : 581.

Heteropelma datanae Riley; Ashmead, 1900 : 581.

[*Heteropelma fulvicorne* (Say); Morley, 1913*a* : 68. Misidentification and incorrect spelling.]

Heteropelma datanae Riley; Morley, 1913*a* : 69.

Heteropelma flavicorne (Brullé); Viereck, 1917 : 285.

Heteropelma flavicorne (Brullé); Schaffner & Griswold, 1934 : 145.

Heteropelma datanae Riley; Schaffner & Griswold, 1934 : 145.

Heteropelma datanae Riley; Haseman, 1940 : 12.
Heteropelma fulvicorne Townes, 1945 : 729. Replacement name for *flavicorne* Brullé. Junior secondary homonym of *Heteropelma fulvicorne* (Cameron), 1899 : 104. **Syn. n.**
Heteropelma fulvicorne Townes; Townes, 1951 : 401.
Tanypelma fulvicorne (Townes) Townes, 1971 : 157.
Tanypelma datanae (Riley) Townes, 1971 : 157.

Description. Lower face 0·80–0·90 times as broad as high; clypeus apically simply convex, in profile flat; mandibles unusually stout, not twisted, the upper tooth subequal in length to the lower. IOD 0·70–0·80 times as long as OOD; posterior ocellus separated from occipital carina by more than 1·50 times ocellar diameter. Head slightly to strongly buccate posteriorly, vertex finely punctate; occipital carina mediodorsally evenly rounded. Flagellum of moderate length, 46- to 55-segmented; 1st flagellar segment 1·65–1·75 times as long as 2nd; interantennal lamella moderately strong, in profile triangular. Face with short pale pubescence.

Pronotum rugosely punctate, anterior hook strong. Mesoscutum punctate, notauli weakly impressed but discernible beyond centre of mesoscutum; mesoscutal pubescence short, pale yellowish. Mesopleuron rather evenly punctate except for smooth postero-dorsal region; epicnemial carina not reaching above lower 0·35 of mesopleuron, not reaching anterior pleural margin; sternaulus weak. Scutellum very convex, rugose. Posterior transverse carina of mesosternum complete. Propodeum reticulate, without lateral projections, ventrally sculptured; propodeum dorsally rather short, 0·60–0·75 times as long as broad.

Mid tibial spurs subequal. Hind leg with basitarsus 0·70–0·85 times as long as tibia, 5·00–6·00 times as long as 2nd tarsal segment; 2nd tarsal segment about 2·00 times as long as 3rd; trochanter about 0·85 times as long as trochantellus ventrally; hind tarsal claw geniculate, basally lobate; ♂ with hind tarsus 2 not ventrally impressed, without broadened macrotrichia but often with densely packed microtrichia.

Wings infumate; CI = 0·90–1·05; MI = 1·35–1·55; ICI = 0·60–2·20; NI = 0·75–0·95. Forewing length 12–17 mm.

Gaster with tergite 2 1·65–1·75 times as long as tergite 3; ♀ with ovipositor about 0·60 times as long as tergite 2.

♂ genitalia. Distivolsella with spines on ventral side of a median ridge. Aedeagus in profile apically subequally bilobate; lateral sclerotized region very broad, apically dilated, indistinctly delineated.

Colour variation. In the southern U.S.A. and in the south-east to about 42°N specimens are reddish brown with the lower face and legs distally paler, whilst in the north-eastern U.S.A. specimens are almost entirely black with only the flagellum yellowish.

Remarks. Examination of material of this species presented a problem not uncommonly encountered in taxonomy. Specimens from lower latitudes are consistently paler coloured than those from the north. Previously the paler form was called *datanae* whilst the darker specimens were considered to be a separate species, *fulvicorne* Townes. Some authors when encountering similar variation in other Hymenoptera have retained the forms as distinct subspecies (Townes, 1957 : 253–256). In the present case the author has not used the subspecies category for the following reasons.

1. Many species of *Heteropelma* with a wide range of geographical distribution exhibit continuous clinal variation in coloration (see p. 168).

2. Both *datanae* and *fulvicorne* are parasites of *Datana* species; indeed both are recorded as parasitizing *D. integerrima* Grote & Robinson (Townes, 1951).

3. The geographical ranges of the two broadly overlap. An unpublished manu-

script by A. B. Gahan (deposited in the USNM) records *fulvicorne* from Virginia whilst *datanae* is recorded as far north as New York.

4. Specimens intermediate between the two colour extremes occur. In the BMNH is a black ♀ with a pale brown face and a ♂ (from New York) with the thorax and most of the gaster black, but with the lower face yellow and the central segments of the gaster and hind legs brown. 1 ♂ from Georgia (UM, Oxford) is uniformly dark brown with the hind legs black and the lower face pale brown.

Some authors regard intergrades between their subspecies as inevitable when there is no geographical barrier present. For example Betrem & Bradley (1971 : 11) when discussing Ethiopian Scoliidae state 'if a species is constantly different from that in an adjoining region it deserves, in our opinion, a subspecific name; the occurrence of intergrades in an intermediate region is to be expected and is not contradictory'. Whilst not wishing to comment on the taxonomic judgement of these authors it must be pointed out that because of the existence of the intergrades in an intermediate region, one extreme population (subspecies) does not adjoin the other extreme population (subspecies) but adjoins the intermediate intergrades from which it does not differ constantly. Such is the case with *H. datanae*. One of the main objects of any taxonomic work must be the production of a workable key to the taxa discussed. If, in the present case, two subspecies of *datanae* were recognized on colour characters, any given key would not work for the intergrades (some 15% of material examined). These specimens would therefore remain indeterminable. The only way the author considers that this can be avoided is by the use of a single taxon, the species *H. datanae*, and including within it the complete range of colour variation.

Host records. Townes (1951) records this species as a parasite of *Datana contracta* Walker, *D. integerrima* Grote & Robinson, *D. ministra* (Drury) and *D. perspicua* Grote & Robinson. Ashmead (1900) records it from *Sphinx luscitiosa* Clemens.

Distribution (Map 2). U.S.A. east of 100°W.

Material examined.

Heteropelma datanae Riley, lectotype ♀, U.S.A.: Virginia, viii. 1880, ex *Datana integerrima* (*T. Pergande*) (USNM). Paralectotypes, 3 ♀, 2 ♂, 1 damaged specimen not sexed, same data as lectotype (USNM); 1 ♀, same data as lectotype (BMNH).

U.S.A.: 1 ♂, Georgia, no further data (UM); 1 ♀, New York, Wappinger Falls, x. 1934 (BMNH); 1 ♀, 1 ♂, New York, no further data (BMNH); 1 ♀, New Hampshire, Monacknock, 1911 (BMNH); 1 ♀, 1 ♂, Rhode Island, Westerley, viii. 1951 (*H. & M. Townes*) (BMNH); 1 ♀, 1 ♂, same data (HKT); 2 ♂, 'America', no further data (BMNH).

Heteropelma nigricorne (Szépligeti) **comb. n.**

(Text-figs 26, 54)

Schizoloma nigricorne Szépligeti, 1906 : 125. Lectotype ♀, India (TM), designated by Townes *et al.*, 1961 : 323 [examined].

Schizoloma nigricorne Szépligeti; Townes *et al.*, 1961 : 323.

Description. Lower face 0·80–0·85 times as broad as high; clypeus angularly rounded, with weak lateral protuberances, in profile swollen; mandibles not twisted, the upper tooth about 2·00 times as long as the lower. IOD 0·60 times as long as OOD; posterior ocellus separated from occipital carina by about 1·00 times maximum ocellar diameter. Head not obviously constricted posteriorly; vertex punctate; occipital carina medio-dorsally evenly rounded, often rather weak. Flagellum elongate, 54- to 55-segmented; 1st flagellar segment 2·30–2·50 times as long as 2nd; interantennal lamella strong, in profile quadrate. Face with elongate pale pubescence.

Pronotum coriaceous, anterior hook strong. Mesoscutum coarsely punctate; notauli moderately impressed, discernible to centre of scutum; mesoscutal pubescence short and pale. Mesopleuron dorsally reticulate, latero-ventrally punctate; epicnemial carina reaching about 0·30 of way up mesopleuron, its upper end distant from anterior pleural margin; sternaulus vestigial. Scutellum longitudinally concave, elongate, punctate. Posterior transverse carina of mesosternum complete. Propodeum coarsely reticulate, without lateral projections, ventrally sculptured; propodeum dorsally about 0·70 times as long as broad.

Mid tibial spurs subequal, the outer about 1·10 times as long as the inner. Hind leg with basitarsus 0·50 times as long as tibia, 2·30–2·40 times as long as 2nd tarsal segment; 2nd tarsal segment 2·90–3·00 times as long as 3rd segment; trochanter subequal to trochantellus ventrally; hind tarsal claws moderately curved, with a weak basal lobe.

Wings infumate; CI = 0·75–0·85; MI = 1·60–1·70; ICI = 0·50–0·60; NI = 0·45–0·55. Forewing length 12–13 mm.

Gaster with tergite 2 2·00–2·10 times as long as tergite 3; ♀ with ovipositor 0·70 times as long as tergite 2.

♂ unknown.

Head black, lower face and marks on genal orbit yellow; flagellum blackish. Thorax and propodeum black, tegulae reddish brown. Legs yellowish brown; anterior two pairs paler than hind pair; hind two pairs of coxae infuscate, hind tibia distally black.

Remarks. This species is similar to some variants of *H. amictum*, especially those which have the lateral clypeal protuberances reduced. However, a number of characters combined in this species have not been observed either to occur at all or in this combination in *H. amictum*. The lower face of this species is more quadrate than that of *H. amictum*. This character combined with the colour of antennae, unusually small value of IOD compared to OOD, complete lack of vertical yellow marks and characteristic clypeal shape serve to distinguish this species from others.

Host records. None available.

Distribution (Map 2). India (peninsular).

Material examined.

Lectotype ♀, India: Matheran, 800 m, 1902 (*Biro*) (TM). Paralectotypes, 2 ♀, same data as lectotype (TM).

Heteropelma amictum (F.)

(Text-figs 12, 13, 16, 17, 18, 42, 46, 61)

Ichneumon amictus Fabricius, 1775 : 341. Holotype ♀ (no further data) (BMNH) [examined].
Ophion amictus (F.) Fabricius, 1798 : 237.
Anomalon amictum (F.) Gravenhorst, 1829 : 650.
Anomalon (*Schizoloma*) *amictum* (F.) Wesmael, 1849 : 120.

Anomalon capitatum Desvignes, 1856 : 104. Lectotype ♂, Great Britain: England (BMNH) designated by Fitton (1976 : 324) [examined]. **Syn. n.**
Schizoloma bucephalum Brauns, 1898 : 71. Holotype ♂ (no further data) (?lost). [Synonymized by Schmiedeknecht, 1908 : 1463.]
Schizoloma fulvicorne Cameron, 1899 : 104. LECTOTYPE ♂, India (UM), here designated [examined]. **Syn. n.**
Anomalon tinctipenne Cameron, 1899 : 112. LECTOTYPE ♀, India (UM), here designated [examined]. **Syn. n.**
[*Anomalon perornatum* Cameron; Szépligeti, 1905 : 12. Misidentification.]
Schizoloma capitata (Desvignes) Szépligeti, 1905 : 34.
Schizoloma amictum (F.); Schmiedeknecht, 1908 : 1462.
Schizoloma capitata (Desvignes); Schmiedeknecht, 1908 : 1463.
Schizoloma amicta (F.); Morley, 1913*a* : 67.
Schizoloma capitata (Desvignes); Morley, 1913*a* : 67.
Schizoloma fulvicornis Cameron; Morley, 1913*a* : 67.
Exochilum acheron Morley, 1913*a* : 79. LECTOTYPE ♀, India (BMNH), here designated [examined]. **Syn. n.**
Anomalon tinctipenne Cameron; Morley, 1913*a* : 83.
Schizoloma fulvicornis Cameron; Morley, 1913*b* : 403.
Schizoloma amictum (F.); Morley, 1913*b* : 404.
Exochilum acheron Morley; Morley, 1913*b* : 412.
Exochilum acheron var. *scutellatum* Morley, 1913*b* : 412. Syntypes ♀ & ♂, India (?Calcutta) [not examined]. **Syn. n.**
Anomalon tinctipenne Cameron; Morley, 1913*b* : 422.
Schizoloma amictum (F.); Morley, 1915 : 276.
Schizoloma capitatum (Desvignes); Morley, 1915 : 227.
Habronyx sachalinensis Matsumura, 1918 : 116. Holotype ♀, Sakhalin (EIHU) [not examined]. [Synonymized by Uchida, 1928 : 233.]
Schizoloma crassicalx Enderlein, 1921 : 11. Holotype ♂, Sumatra (IZPAN) [examined]. **Syn. n.**
Schizoloma amictum (F.); Uchida, 1928 : 233.
Schizoloma amictum var. *nigricoxalis* Uchida, 1928 : 234. Lectotype ♀, Sakhalin (EIHU), designated by Townes *et al.*, 1965 : 383 [not examined]. [Synonymized by Uchida, 1958 : 91.]
Schizoloma amictum var. *intermedium* Uchida, 1928 : 234. Lectotype ♂, Japan (EIHU), designated by Townes *et al.*, 1965 : 383. [Synonymized by Uchida, 1958 : 91.]
Schizoloma coreanum Uchida, 1928 : 235. LECTOTYPE ♂, Korea (EIHU), here designated [examined]. **Syn. n.**
Schizoloma amictum (F.); Schmiedeknecht, 1936 : 63.
Schizoloma capitatum (Desvignes); Schmiedeknecht, 1936 : 64.
Schizoloma amictum (F.); Uchida, 1958 : 90.
Schizoloma coreanum Uchida; Uchida, 1958 : 91.
Schizoloma amictum (F.); Townes *et al.*, 1961 : 322.
Schizoloma capitatum (Desvignes); Townes *et al.*, 1961 : 323.
Schizoloma crassicalx Enderlein; Townes *et al.*, 1961 : 323.
Schizoloma fulvicorne Cameron; Townes *et al.*, 1961 : 323.
Schizoloma tinctipenne (Cameron) Townes *et al.*, 1961 : 323.
Heteropelma acheron (Morley) Townes, Momoi & Townes, 1965 : 382.
Schizoloma amictum (F.); Townes, Momoi & Townes, 1965 : 383.
Schizoloma capitatum (Desvignes); Townes, Momoi & Townes, 1965 : 384.
Schizoloma coreanum Uchida; Townes, Momoi & Townes, 1965 : 385.
Heteropelma amictum (F.) Townes, 1971 : 157.

Description. Lower face 0·55–0·70 times as broad as high; clypeus apically usually with strong lateral protuberances, rarely with these weak; clypeus in profile swollen to excised;

mandibles twisted about 10°, the upper tooth usually about 2·00 times as long as lower; IOD 0·65–1·05 times as long as OOD; posterior ocelli closer to occipital carina than maximum ocellar diameter. Head of ♀ slightly narrowed posteriorly, ♂ from similar to that of ♀ to extremely buccate; vertex punctate; occipital carina medio-dorsally rounded or flattened. Flagellum of moderate length, 52- to 63-segmented; 1st flagellar segment 2·00–2·50 times as long as 2nd; interantennal lamella strong, in profile quadrate. Face with moderately long pale pubescence.

Pronotum punctate, anterior hook strong. Mesoscutum usually punctate; notauli vestigial to distinctly impressed; pubescence of mesoscutum yellowish. Mesopleuron dorsally coriaceous, latero-ventrally punctate; epicnemial carina reaching 0·30–0·50 of way up mesopleuron, usually with upper end indistinct and not reaching anterior pleural margin. Scutellum usually longitudinally concave, rarely with concavity weak, elongate to subquadrate, usually coarsely punctate. Posterior transverse carina of mesosternum complete. Propodeum reticulate, ventrally sculptured; dorsally 0·70–0·95 times as long as broad, without lateral protuberances.

Mid tibial spurs approximately equal in length. Hind leg with basitarsus 0·44–0·54 times as long as tibia, 1·60–2·30 (isolated specimens up to 2·80) times as long as 2nd tarsal segment; 2nd tarsal segment 1·60–2·30 times as long as 3rd; trochanter 0·70–0·90 times as long as trochantellus ventrally; hind tarsal claw geniculate, rarely less strongly curved and with the normally strong basal lobe weaker, 2nd hind tarsal segment of ♂ with strongly impressed ventral area.

Wings infumate weakly; CI = 0·68–1·10; MI = 1·40–2·10; ICI = 0·20–0·90; NI = 0·45–0·65. Forewing length 7–16 mm.

Gaster with tergite 2 2·00–2·30 times as long as tergite 3; ♀ with ovipositor 0·50–0·60 times as long as tergite 2.

♂ genitalia. Distivolsella with spines arranged in apical cluster and with a short row of double spines on ventral margin. Aedeagus in profile apically subequally bilobate; lateral sclerotized region broad, apically dilated, indistinctly delineated.

Head black, lower face, vertical marks and genal orbital marks yellow. Thorax black, tegulae usually reddish, very rarely with tegulae, subalar prominences, and occasionally also scutellum yellowish. Anterior two pairs of legs yellow; hind legs reddish, always with tibia distally and often coxae in part, sometimes also femur dorsally blackish; hind tarsi yellowish.

Variation. This species previously was divided into a number of separate species which, together with *H. nigricorne*, were placed in a separate genus, *Schizoloma*. Townes (1971) treated *Schizoloma* as a synonym of *Heteropelma* and Gauld (1976) concurred with this opinion. In the present work all species catalogued by Townes *et al.* (1961; 1965) as *Schizoloma* (except *H. nigritarse*) and one species catalogued as *Heteropelma* (*H. acheron*) are treated as synonyms of *H. amictum*.

This lumping of species is a rather different approach from that currently employed by many Ichneumonologists, who favour a very narrow species concept and frequently make use of the subspecies category (Gupta, 1962; Townes & Chiu, 1970). Because of this contravention of established procedure a detailed discussion of character variation is included.

Townes and co-workers (1961; 1965) have catalogued six species which here are reduced to synonymy. Comparison of the original descriptions and examination of available keys (Morley, 1913*a*; 1913*b*; Schmiedeknecht, 1936; Uchida, 1958) has enabled the author to select those characters which have been used to facilitate specific separation. Study of extensive material has enabled the relative taxonomic merits of these characters to be assessed.

The following characters have been used to facilitate specific separation or show

a great deal of variation and therefore may possibly be of use to effect specific separation:

1, gross head shape; 2, structure of clypeo-mandibular region; 3, head colour; 4, antennal colour; 5, microsculpture of vertex; 6, microsculpture of mesonotum; 7, sculpture of propodeum; 8, relative lengths of hind tarsal segments; 9, colour of hind legs; 10, wing venation; 11, scutellar colour; 12, shape of hind tarsal claw; 13, geographical distribution.

These characters are individually discussed below.

1. Gross head shape. Sexual dimorphism in head shape is not uncommon amongst species of the Ichneumonidae and is particularly obvious in some Therionini. This discussion is concerned only with the gross head shape of the males, which typically have the head somewhat more buccate than that of the corresponding females.

Desvignes (1856) described *H. capitatum* from a pair of males which he separated from *H. amictum* by the much more buccate head (Text-figs 12, 13). Although extensive collecting has been undertaken since, no truly intermediate specimens have been discovered. It is therefore quite feasible to regard the two as distinct species as have all previous authors. There are, however, several reasons which have lead the author to believe that *H. capitatum* is conspecific with *H. amictum*. These are as follows.

(a) The females of the species are wholly indistinguishable.

(b) The species are synchronous and sympatric. *H. capitatum* has only been taken occasionally (*ca* 10%) in areas which support a large population of *H. amictum*, such as heathlands (in the Anomaloninae closely related species frequently manifest clear differences in habitat preference. For example *Agrypon anxium* (Wesmael) prefers open hedgerows whilst *A. variitarsum* (Wesmael) is restricted to shaded woodlands).

(c) No consistent differences have been observed in other morphological characters, including genitalia structure.

(d) Although only limited material is available there is apparently no difference in host preference.

(e) The geographical range of the two species almost exactly coincides.

Towards the centre of the range of geographical distribution in the Indo-Malayan region, the incidence of 'buccate headedness' within a population increases. This variation in incidence of buccate headedness of geographically separated populations is tabulated below.

LOCALITY	No. EXAMINED	% BUCCATE HEADED
England: Exmoor	27	10
Nepal: Tapeljung	9	33
Burma: Nam Tami	9	70
Japan: Kamikochi	17	12
Java: Tjibodas region	16	7

(some intermediates were observed in the Japanese population)

Whilst much larger samples must be examined before any reliable inferences can be drawn concerning the variation of incidence of 'buccate headedness' between the populations, it is probably reasonable to suggest that there is a considerable variation in the frequency of 'buccate headedness' between the several populations.

The shape of the ocellar triangle was observed to vary between specimens but this variation was apparently linked to that of the head shape. In specimens with buccate heads the ocellar triangle was approximately equilateral (consequently the anterior angle would be 60°) whilst the specimens without a buccate head were observed to have the ocellar triangle posteriorly broadened (with the anterior angle at or more than 90°).

It may be concluded that gross head shape and shape of the ocellar triangle are not reliable characters for effecting specific separation, as in most populations studied variations of the characters were observed. It is possible that the difference between the simple and buccate headed forms is a single, or relatively few, gene difference as intermediate forms are so uncommon.

In buccate headed specimens there was found to be a much greater development of the adductor muscles of the mandibles. It is possible that having these muscles relatively stronger is a selective advantage in certain areas. As the only apparent function of the Ichneumonid mandibles is to effect escape from the host puparium one might expect that in specimens pupating in large hosts with a strong puparium the possession of exceptionally strong mandibular muscles would be a selective advantage. In other regions where such a host is less common and the principal host is a smaller species with a weaker puparium the possession of a buccate head would not bestow any selective advantage, indeed may even be disadvantageous. Thus one would expect variation in the frequency of buccate headedness between populations.

2. Structure of the clypeo-mandibular region. Morley (1913*a*) separated *acheron* from other species placed in *Schizoloma* on account of the difference in clypeo-mandibular structure. In '*Schizoloma*' the lateral corners of the clypeus are produced until in extreme cases these lateral protuberances entirely conceal the clypeal margin except for a narrow median cleft. In *acheron* and a number of other specimens examined the lateral protuberances were observed to be very weakly developed. Examples of such specimens have been taken in Burma, India, South Korea, Japan and Taiwan. There are three obvious interpretations of the available material.

(a) All represent variants of *H. amictum*.
(b) All are conspecific and represent a distinct species *Heteropelma* X.
(c) All represent distinct species *Heteropelma* B, I, K, J, & T respectively.

To enable further evaluation of the above hypotheses the specimen groups B, I, K, J & T were compared with typical *H. amictum* specimens from neighbouring localities. These data are presented in Table 1.

In each case excluding that of the Japanese specimens, the variants were found to resemble *H. amictum* in all except a single additional feature. The characters tabulated were chosen because they are of use in separating a number of species within this genus. If hypotheses b or c were applicable one would have expected

TABLE 1

A comparison of critical features of variants of *Heteropelma amictum*

VARIANT	CLYPEUS	NUMBER OF FLAGELLAR SEGMENTS	FLAGELLUM COLOUR	MI	CI	RATIO OF 1st TO 2nd HIND TARSI	COLOUR OF HIND COXA	NUMBER OF SPECIMENS EXAMINED
H. amictum (Japan, Kamikochi)	normal	51–57	Red, distally paler proximally darker	1·55–1·80	0·74–0·95	1·60–2·10	Variable black to reddish yellow	18
Heteropelma 'J' (Japan, Hanamaki)	weakly produced	58	as above	1·80–1·90	0·80–0·90	1·60–1·70	Yellow ventrally blackish	2
H. amictum (Korea, Kainai)	normal	55	Reddish yellow	1·60	0·80	1·70	Yellow and badious	1
Heteropelma 'K' (Korea)	moderately produced	50	as above	1·60–1·80	0·80–0·85	1·70–2·20	Reddish yellow and badious	2
H. amictum (India, Simla)	normal	51–58	Red, distally paler proximally darker	1·60–1·75	0·75–0·95	1·70–2·30	Red	8
Heteropelma 'I' (India, Simla)	weakly produced	53–55	as above	1·55–1·75	0·75–0·95	2·10–2·80	Red	6
H. amictum (Burma, Nam Tamai Valley)	normal	54–59	as above	1·45–1·90	0·70–0·95	1·60–2·30	Red	14
Heteropelma 'B' (Burma, Mt Victoria)	very weakly produced	—	as above	1·50–1·70	0·60–0·75	1·80–2·20	Red	4
H. amictum (Taiwan)	normal	52–63	as above	1·60–1·90	0·75–0·85	1·70–2·10	Red	4
Heteropelma 'T' (Taiwan)	weakly produced	50–52	as above	1·70–2·00	0·75–0·85	2·00	Reddish yellow and badious	2

differences in more characters. If b were applicable one would expect more similarity between B, I, K, etc., than these show to *H. amictum*. This is not the case.

Only in the case of 'J' were differences found in more than one additional character. As this group was represented by only a pair of male specimens investigations could not be taken further.

Examination of the available material has shown that reduction of the clypeal protuberance differs in many of the specimens and it is possible to construct a series showing progressive reduction from normal to extremely weakly produced (Burma: Mt Victoria).

As the specimens with the weakly produced clypea were otherwise found to be so similar to typical *H. amictum* specimens and differences where observed were almost always found to be within the range of variation expected for the species as a whole, it is concluded that these specimens represent variants of *H. amictum* (that is accept hypothesis a). The specimens therefore do not warrant separate specific status.

Accompanying the variation in the shape of the clypeus is a variation in the shape of the mandibles. Those of the typical *H. amictum* specimens were observed to be stouter and slightly more twisted than those of the specimens with reduced clypeal protuberances. Variation in clypeal shape amongst the Therionini is invariably accompanied by variation in the mandibular shape. In the present work therefore these are regarded as linked characters so the remarks made concerning the clypeal variation are equally applicable to mandibular variation.

3. Head coloration. Morley (1913*a* : 66) separated *H. amictum* from other species on account of its immaculate vertical orbits. The present author has seen no specimens with immaculate vertical orbits although he has examined Morley's collection. Typically the head was observed to be black with the lower face yellow. Two yellow marks were invariably present on each orbit, one on the vertex and the second just above the centre of the gena. The extent of these marks was observed to vary in the material examined. In some cases the vertical mark was seen to be confluent with the facial area of yellow, but generally the two were discrete.

It must therefore be concluded that the differences in head coloration are of no use for separating *H. amictum* from the 'species' included here as synonyms.

4. Antennal coloration. Cameron (1899) described *fulvicorne* as having the flagellum more evenly fulvous than that of typical *H. amictum*.

Almost all specimens examined were observed to have the antennae reddish, distally yellow, basally externally darker and internally yellowish. In some specimens from the Indo-Malaysian region the yellow areas were less apparent (vide *fulvicorne*). Some Japanese specimens have been observed to have the basal segments of the antennae black. Philippino specimens were observed to have the antennae more or less entirely badious whilst those of Indonesian specimens were entirely black except for one specimen with the extreme distal apex reddish and the base internally yellow marked. Occasional specimens from other regions have similarly marked antennae.

From these observations it may be deduced that antennal coloration may be

of some use in separating populations but that the status of these segregates must remain questionable until more characters are examined.

5. Microsculpture of the vertex. Study of species descriptions would lead one to expect that there might be differences between the vertical sculpture of several of the 'species' catalogued as *Schizoloma*.

Most specimens were observed to have the vertex punctate. Some variation in size and density of the puncturation was observed but it was noted that the larger the individual the proportionally more widely separated the punctures were found to be. Consequently more similarity in vertical sculpture was observed between large individuals of geographically widely separated populations, than between large and small specimens of the same population.

Microsculpture of the vertex was not considered to be a useful character to facilitate specific separation.

6. Microsculpture of the mesoscutum (mesonotum of authors). Uchida (1958 : 90) distinguished *H. coreanum* from *H. amictum* by differences in mesoscutal puncturation. The former was described as having the mesoscutum 'ganz matt, dicht fein punktiert' whilst that of the latter was described as 'grösser und zerstreuter als beim *coreanum*'. The author has examined the lectotype of *coreanum* and observed that the puncturation of the mesoscutum is indeed more dense than is usual in *H. amictum*. The puncturation of the mesoscutum of the female paralectotype is far more like that of *H. amictum*. There is no other consistent difference between *coreanum* and *amictum*, and as there is a considerable range of variation of density of puncturation of the mesoscutum within *H. amictum* it is suggested that the puncturation of *H. coreanum* is an extreme variation of the range of that of *H. amictum* and that it is therefore justifiable to include this species as a synonym of *H. amictum*.

7. Sculpture of the propodeum. Differences in propodeal sculpture have been used by Morley (1913*a* : 66; 1915 : 226) and Uchida (1958 : 90) to separate *H. capitatum* from *H. amictum*. That of the former is described as 'radiating from the centre' whilst that of the latter is said to 'form areae'.

A very large range of variation in the complex sculpture patterns of the propodea of *Heteropelma* species have been observed. Large specimens invariably tend to have extremely coarse reticulations with far more enclosed areae. Propodeal sculpture is therefore not considered to be useful in classifying species of *Heteropelma*.

8. Relative length of the hind tarsal segments. Reference to relative length of the 1st and 2nd hind tarsal segments in species descriptions are generally inaccurate approximations. Thus it appears that there may be differences in the ratios of tarsal lengths between the various described entities considered here.

No differences were observed between males and females (other than the broadening of the male tarsi which in a superficial examination may give the impression that the tarsi are proportionally shorter than those of the female). All specimens examined were found to have the hind basitarsus between 1·60 and 2·80 times as long as the second tarsal segment with a mean of 1·92.

9. Colour of hind legs. Typically the legs are yellowish red with the coxae and trochanteral segments paler ventrally, coxae proximally and distal 0·3 of tibiae

blackish. The tarsi are immaculately yellow. This colour pattern is fairly constant throughout the European and Indo-Malayan ranges of distribution, with the latter sometimes having the proximal segments less clearly pale marked ventrally.

The coxal colour was observed to be more variable. One group of specimens from Nepal showed a range of colour variation. Some specimens had the coxae red with the extreme proximal margins black, other specimens were intermediate and some extreme specimens were observed to have the coxae entirely black. Similar variation has been observed in Japanese species.

In some specimens the coxae were observed to be very dark except for the ventral area which was yellow marked. Such specimens were usually, but not always, observed to have the femora badious dorsally. This colour pattern was most common in specimens from Java, Sumatra and the Philippines, although isolated specimens from other regions also exhibit a similar colour pattern.

A single specimen from Sulawesi was observed not to have the hind tibia dark marked distally.

From these observations one may conclude that coloration of the hind legs alone is not a suitable character for specific separation, but that this colour patterning may be of use in segregating groups of specimens from different regions.

10. Wing venation. Morley (1913*a* : 66; 1913*b* : 403; 1915 : 226) used features of wing venation to facilitate species separation. In the two earlier works he used the position of the internal cubital (i.e. 1*m–cu*) with respect to its point of contact with 2 + 3*rm*/*M*. In this work this position is quantified by the inter-cubital

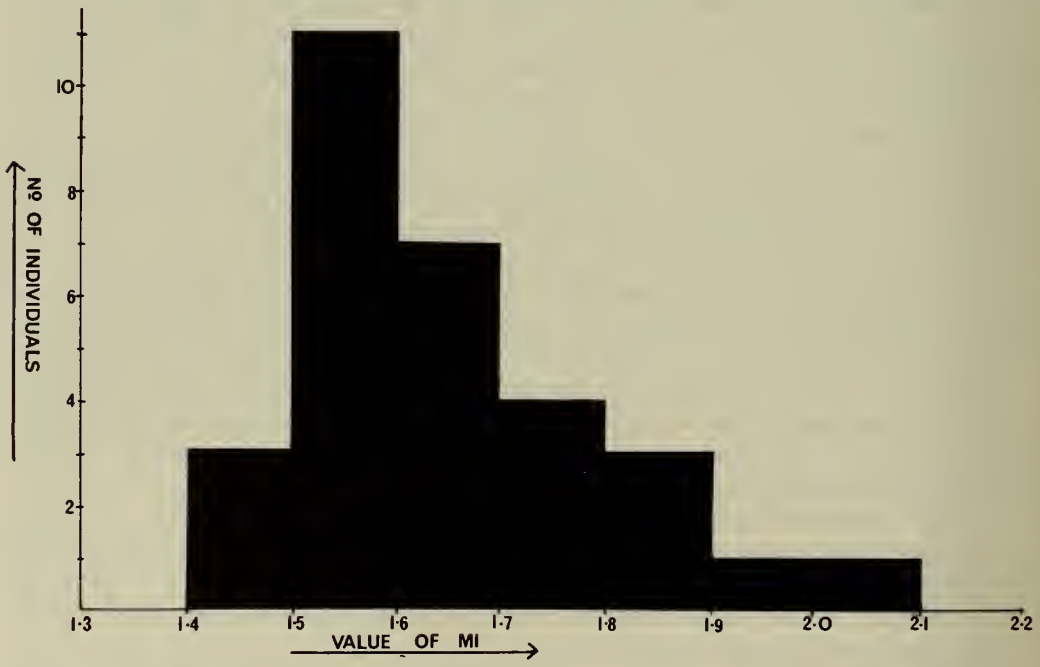


Chart 1. Histogram showing the range of values of MI in *Heteropelma amictum*. [Class width = 0·1; sample number 15 ♀, 15 ♂].

index ICI. In the latter work Morley used the shape of the radial cell to distinguish two species. This shape is quantified by the marginal index MI.

Values of the marginal index are shown in Chart 1. These values were obtained from the measurement of thirty specimens (15 ♀, 15 ♂) from the Palaearctic/Indo-Malayan regions. Of the specimens measured 7 ♂ were clearly referable to *capitatum* whilst 8 were typical *amictum*. It can be seen from the chart that there is no indication of a bimodal distribution of values. Such a bimodal distribution would be expected if two species differing in values of MI had been confused. It may be assumed therefore that the value of MI is not a reliable character for the separation of species.

The cubital cross vein region of the forewing of Anomaloninae is an area of morphological 'instability' (i.e. one often encounters considerable intraspecific variation in this region, see Gauld (1976)). Measurement of the ICI was undertaken for a number of typical specimens of *H. amictum* and for a number of buccate headed specimens. The results are given below.

	No. MEASURED	RANGE OF ICI	MEAN
typical *H. amictum*	15	0·2–0·8	0·55
buccate headed specimens	15	0·3–0·9	0·60

It may be deduced that there is no significant difference between the values of ICI. This character is therefore of no use in facilitating specific separation.

11. Colour of scutellum. Isolated specimens have been found to have the scutellum yellow. No other consistent morphological differences were observed between these specimens and typical specimens of *H. amictum*.

12. Shape of hind tarsal claws. In *H. amictum* as in most other species of *Heteropelma* the hind tarsal claws are typically geniculate and basally lobate. In the south-east of the range of distribution some specimens have been observed to have modified claws, that is with the basal lobe reduced. The Javan population was found to have a high incidence of this modification. Of the 18 specimens examined only 4 were found to have normally lobate claws.

However, because there is variation in this character it is alone not suitable for facilitating specific separation.

13. Geographical distribution. From the material available it has been established that this species extends from Britain throughout the Palaearctic region to Japan, along the Himalayas into southern China, Taiwan and the Philippines and also in Burma, Sumatra, Java and Sulawesi (Map 2).

Ichneumonidae have not been extensively collected and in the past authors tended to regard specimens collected by expeditions to relatively unworked areas as new. Such specimens are described as species novae and the description serves to distinguish them from the better known (usually Palaearctic) species of the genus. Such is the case in question. Numerous species of '*Schizoloma*' have been described from very little material and generally each differs slightly from other described entities. The problem presented here is whether or not these entities deserve specific status. Examination of fairly extensive material from the above

Map 2. The world (Mercator projection) showing distributions of *Heteropelma amictum*, *H. scaposum*, *H. flavitarse*, *H. nigricorne*, *H. datanae* and *H. townesi*.

mentioned countries has indicated that there is a large range of variation in several 'critical' characters even within a population and that the extent of this variation broadly overlaps that of populations in neighbouring countries. When considering the range of distribution as a whole, widely separated populations were found to exhibit quite different frequencies of the various character conditions. Such differences within a species of broad geographical distribution are to be expected and such clinal variation has been fully discussed by a number of authors (Huxley, 1939; Crowson, 1970).

No standard way of designating such clinal variation has been adopted. Huxley (1939) suggested the naming of only the end forms and using formulae to indicate various intermediates. This method has not been adopted by subsequent workers nor is it covered by the current *International Code of Zoological Nomenclature*. Additional complications are introduced in the present case as the eastern end of the distribution of *H. amictum* is apparently bifurcate.

Using the variations of clinal gradient to delimit natural subspecies (as suggested by Crowson, 1970) is not possible in the present case as insufficient material is available for study.

The present author's approach to the outlined clinal variation is to refrain from designating any population as a subspecies of *H. amictum*.

The status of one population deserves further consideration. A group of 18 specimens from Java were observed to be rather distinct from the remainder of the species. The Javanese specimens were found to have a low percentage incidence of buccate headedness, to generally have the flagellum black, to have the hind

femora black marked and to have a high incidence of weakly lobate hind tarsal claws. If clinal gradient may be expressed as a formula of the form, number of character conditions found in 80% of the population A and observed in less than 20% of population B, divided by the linear distance separating the two populations plotted against the linear distance separating the two populations, then the gradient between the Burmese population and the Javan population would be greater than that between the former, and either the European or Japanese populations. This would seem to indicate that the Javan population may deserve separate subspecific status. However, no specimens from the intermediate areas of the Malay peninsula are available for study and only a single specimen from Sumatra was seen. This Sumatran specimen, whilst having many features of the Java population, was observed to have geniculate claws and a buccate head. For the present, therefore, the Javan population is included within *H. amictum* and not accorded subspecific status.

A similar approach was adopted by Perkins (1953) in his work on the British Ichneumoninae. Although he mentions (p. 117) that there are minor differences between the British examples of a species and conspecific European specimens he did not elevate the British population to separate subspecific status.

Unfortunately in this work it has only been possible to study the morphology of the adult insect extensively. Such an approach is not wholly adequate when investigating such complex clinal variation. From consideration of the data presented above it has been suggested that all specimens are better retained within a single species, *H. amictum*. It is not inconceivable that there may be marked differences in the habitat preference, host selection, behavioural patterns and larval structure between some of the populations. Such data, if and when they become available, may be found to correlate with geographical and character state frequency differences mentioned above. In such a case it may be necessary to reconsider the classification herein proposed.

Host records. This species has been recorded as a parasite of the following lepidopterous larvae: *Bena prasinana* (L.) (Meyer, 1935; Schmiedeknecht, 1935); *Callimorpha dominula* (L.) (Meyer, 1935; Schmiedeknecht, 1935); *Dasychira pudibunda* (L.) (Uchida, 1928; 1958; Meyer, 1935; Schmiedeknecht, 1935); *Dendrolimus albolineatus* Matsumura (Matsumura, 1926; Uchida, 1928); *D. sibiricus* Tschetverikov (Matsumura, 1926); *D. spectabilis* (Butler) and *D. superans* (Butler) (Uchida, 1958); *Eupithecia linariata* (Denis & Schiffermüller) (Meyer, 1935; Schmiedeknecht, 1935); *Hyloicus pinastri* (L.) (Meyer, 1935); *Lacanobia oleracea* (L.) (Morley, 1915); *Lathoe populi* (L.) (Meyer, 1935; Schmiedeknecht, 1935); *Lithophane ornitopus* (Hufnagel) (Meyer, 1935; Schmiedeknecht, 1935); *Macrothylacia rubi* (L.) (Meyer, 1935; Schmiedeknecht, 1935); *Phalera bucephala* (L.) (Meyer, 1935; Schmiedeknecht, 1935); *Polia nebulosa* (Hufnagel) (Morley, 1915); *Thaumatopoea processionea* (L.) (Meyer, 1935; Schmiedeknecht, 1935).

Distribution (Map 2). This species has been recorded from most northern European countries (Morley, 1915; Schmiedeknecht, 1935) but is possibly absent from the Mediterranean basin as Ceballos (1963) failed to record it from Spain.

It has been recorded from Japan, Korea, Kuriles, Sakhalin and Formosa (Uchida, 1928; 1958), and widely from the U.S.S.R. (Meyer, 1935). In the Oriental region it has been recorded from India and Burma (Morley, 1913*b*) and from Sumatra (Enderlein, 1921).

MATERIAL EXAMINED.

Ichneumon amictum Fabricius, holotype ♀, no further data (BMNH). *Anomalon capitatum* Desvignes, lectotype ♂, GREAT BRITAIN: England, no further data (BMNH); (depository of paralectotypes unknown). *Anomalon tinctipenne* Cameron, lectotype ♀, INDIA: Assam, Khasia Hills (UM); paralectotypes 3 ♀, 1 ♂, same locality as lectotype (BMNH); 4 ♀, 1 ♂, same locality as lectotype (UM). *Schizoloma fulvicorne* Cameron, lectotype ♂, INDIA, no further data (UM); 1 ♂, ? paralectotype, no data (UM). *Exochilum acheron* Morley, lectotype ♀, INDIA: 1851 (*Baly*) (BMNH); paralectotypes 2 ♀, 3 ♂, INDIA: 1851 (BMNH) [Townes *et al.* (1961) state that the type depository of *acheron* is the UM (Oxford). The author has examined the collections in the UM and has seen no specimen that could have indisputably been before Morley when he described this species. However, there are in the BMNH 3 ♀, 3 ♂ labelled in 1910 by Morley as *Exochilum acheron* and from the appended locality data it was clearly apparent that these specimens were syntypes. An intact female was therefore selected as lectotype.] *Schizoloma crassicalx* Enderlein, holotype ♂, SUMATRA: no further data (IZPAN). *Schizoloma coreanum* Uchida, lectotype ♂, KOREA: no further data (EIHU).

BELGIUM: 1 ♀, no further data (BMNH); 1 ♀, 1 ♂, no further data (IRSNB). BURMA: 2 ♀, 2 ♂, Mt Victoria xii–iv. 1937–38 (*Heinrich*) (HKT); 1 ♀, 1 ♂, Nam Tamai, xi. 1931 (*Cranbrook*) (BMNH); 4 ♀, 8 ♂, Nam Tamai Valley, viii–ix. 1938 (*Kaulback*) (BMNH); 1 ♀, 1 ♂, Nam Tisong, i. 1931 (*Ward*) (BMNH). CHINA: 2 ♀, 2 ♂, Fukien, Shaowu Hsien, vi–x. 1943–45 (*Maa*) (HKT); 1 ♂, Kiangsi, Hong San, vii. 1936 (HKT); 2 ♂, Szechwan, Kwan, viii. 1938 (HKT). GERMANY: 1 ♀, Berlin, no further data (BMNH); 2 ♀, 2 ♂, no data (BMNH); 1 ♀, no data (IRSNB). GREAT BRITAIN: 1 ♀, Cheshire, Delamere Forest, 1904 (BMNH); 1 ♀, 1 ♂, Cumbria, Witherslack, vii. 1922, ex *Polia nebulosa* (Hufnagel) (*Lowther*) (BMNH); 20 ♀, 27 ♂, Devon, Exmoor, viii. 1971 (*Gauld*) (BMNH); 7 ♀, 5 ♂, Devon, no further data (BMNH); 2 ♀, 5 ♂, Grampian 'Aberdeenshire', Glen Muick, vii. 1975 (*Gauld*) (BMNH); 1 ♀, 1 ♂, Highland 'Inverness-shire', Aviemore, vii. 1929 (*Harwood*) (BMNH); 1 ♂ no locality data, ex *Cucullia* sp. (*Bond*) (BMNH); 7 ♀, 5 ♂, no data (BMNH). INDIA: 4 ♀, 6 ♂, 'Northern India', no further data (UM); 1 ♀, 1 ♂, Simla, viii. 1918 (*Brunetti*) (BMNH); 1 ♂, no data (BMNH). IRELAND: 1 ♂, Eire, Bantry, viii. 1909 (*Fletcher*) (BMNH). JAPAN: 2 ♂, Hanamaki, Iwate, vi. 1953 (*Sato*) (HKT); 1 ♀, 17 ♂, Kamikochi, vii. 1954 (*Townes family*) (HKT); 2 ♀, 1 ♂, Mt Norikura, vii. 1954 (*Townes family*) (HKT); 1 ♂, Mt Wakasugi, ii. 1927 (*Yasamatsu*) (HKT); 3 ♀, Sapporo, vii. 1954 (*Townes family*) (HKT); 1 ♀, Yamanischi, vi. 1927 (HKT); 1 ♂, no data (*Matsumura*) (HKT). JAVA: 1 ♀, 1 ♂, Dgampang Mts, ix. 1938 (*Bengbreng*) (BMNH); 1 ♂, Digeenoeng, Dgampang Tengah, 1939+ (HKT); 1 ♂, Gunung, Gedeh, viii. 1937 (*Sloe*) (BMNH); 1 ♀, Mt Gede, i. 1935 (HKT); 1 ♂, Nougkodyadjar, v. 1938 (*Walsh*) (BMNH); 3 ♀, 4 ♂, Tjibodas, Gedeh, 1930–7 (*Leftinck*) (HKT); 2 ♂, Tjibodas,

viii. 1934 (*Handschin*) (BMNH); 1 ♀, 1 ♂, Tjibodas, iii. 1916 (*Robinson*) (BMNH); 1 ♀, no further data (IRSNB). KOREA: 1 ♂, vii. 1931 (*Sato*) (HKT). NEPAL: 1 ♀, 9 ♂, Taplejung, between Sangu and Tamrang, x–xi. 1961 (*Coe*) (BMNH). PHILIPPINES: 1 ♂, Abra, Basiwa, iii. 1953 (*M. C. Townes*) (HKT); 3 ♂, Kalinga, Babalasang, iii. 1953 (*M. C. Townes*) (HKT). SULAWESI: 1 ♀, Todjambol, vii. 1936 (*Toxopeus*) (HKT). SWEDEN: 1 ♀, 1 ♂, Kivik, vii. 1938 (*D. M. S. & J. F. Perkins*) (BMNH). TAIWAN: 1 ♀, Arisan, vi. 1931 (*Gressitt*) (HKT); 1 ♂, Kuraru, vi. 1934 (*Gressitt*) (HKT); 1 ♂ Matsumine, v. 1932 (*Gressitt*) (HKT); 1 ♂, Sakashen, vii. 1934 (*Gressitt*) (HKT). U.S.S.R.: 4 ♀, 3 ♂, Kiev, no further data (IRSNB); 1 ♂, Vladivostok (*Tosquinet*) (IRSNB).

RELATIONSHIPS BETWEEN THE SPECIES

It is not within the scope of a work such as this to discuss the relative merits and shortcomings of phenetic versus phylogenetic classification. It is the opinion of the author that both approaches may be of some use in expanding our knowledge of various groups. In this work therefore phenetic and phylogenetic classifications of the species of *Heteropelma* are discussed separately below.

PHENETIC INTERRELATIONSHIPS. From the species under consideration a large number of characters were considered and those showing little or no inter-specific variation were eliminated. The remaining forty characters were considered to be representative of the interspecific variation. These characters were formulated so as to allow an insect to be scored as either + or —. This system of scoring is not meant to infer that a + character is in any way more significant than a — one. In a few cases intermediates have been found and these were scored ± and were not considered to differ from a + or a — character. In a very few cases full information was not available because of lack of material of one or other sex. In these cases percentage similarities were calculated for the number of scored characters compared.

The characters used together with their + and — alternatives are listed below.

CHARACTER	+	—
1. Clypeal shape	flat	laterally swollen
2. IOD in relation to OOD	greater than	equal to or less than
3. No. of flagellar segments	49 or less	50 or more
4. Gross head shape	constricted	not constricted
5. Occipital carina dorsally	concave	flat or convex
6. Yellow vertical marks	present	absent
7. Interantennal lamella	quadrate	not quadrate
8. Facial pubescence	white or yellow	black or reddish
9. Female facial colour	entirely yellow	not entirely yellow
10. Width of lower face compared with height	0·79 or less	0·80 or more
11. Pronotal hook	strong	vestigial
12. Notauli	present	absent
13. Mesoscutum centrally	coriaceous	punctate

CHARACTER	+	−
14. Height of epicnemial carina in relation to 0·4 of height of mesopleuron	at or above	below
15. Upper end of epicnemial carina	reaching anterior pleural margin	not reaching anterior pleural margin
16. Sculpture of latero-ventral part of mesopleuron	coarsely punctate	finely punctate
17. Sternaulus	strong	weak
18. Scutellum in profile	flat	humped
19. Posterior transverse carina mesosternum	complete	incomplete centrally
20. Propodeal projections	present	absent
21. Propodeum ventrally	smooth	sculptured
22. Propodeum dorsally	0·9– as long as broad	0·91+ as long as broad
23. Colour of thorax	black	not black
24. Colour of scutellum compared with mesoscutum	contrasted	concolorous
25. Mid tibial spurs	subequal	inequal or one absent
26. Hind basitarsal length	3·00+ times length of tarsus 2	2·99– times length of of tarsus 2
27. Hind trochanter length	0·91+ times length of trochantellum	0·90– times length of trochantellus
28. Shape of hind tarsal claw distally	geniculate	simply curved
29. Shape of hind tarsal claw basally	strongly lobate	weakly lobate
30. Impressed area on male hind tarsus 2	present	absent
31. Colour of hind basitarsus	entirely yellow	not entirely yellow
32. Wing colour	black	not black
33. CI	0·80–	0·81+
34. MI	2·00–	2·01+
35. NI	0·50–	0·51+
36. ICI	0·30–	0·31+
37. Tergite 2 length compared with that of tergite 3	2·00+	1·99–
38. Tergite 3 length compared with that of tergite 4	0·80–	0·81+
39. Aedeagal apex	subequally bilobate	not equally bilobate
40. Occipital carina dorsally	complete	incomplete

By comparison of the various species scored percentage similarities were calculated and these values were tabulated in the form of a similarity matrix (Table 2). From these results an average linkage dendrogram was produced (Chart 2) using the unweighted paired group method (UPGMA) of analysis. Thus

$$S_{(abc),\,d} = \tfrac{1}{3}\,(S_{a,\,d} + S_{b,\,d} + S_{c,\,d})$$

where S = similarity and a, b, c, & d represents species.

It can be seen from the dendrogram that *H. celeno* and *H. aello* have comparatively few characters in common with the remainder of the genus. In the 74–76%

similarity range the greater part of the genus divides into two species-groups, the *H. calcator* and *H. amictum* species-groups. Several species separate singly (*H. flavitarse, H. savaiiense, H. datanae* and *H. townesi*).

CHART 2. Dendrogram showing phenetic interrelationships of species of *Heteropelma*.

PROPOSED PHYLOGENETIC INTERRELATIONSHIPS. In any attempt to elucidate the phylogeny of a group (in the absence of a fossil record) the principal source of error is the separation of ancestral characters from derived ones. For example, in *Heteropelma* the absence of an inter-antennal lamella could either be regarded as an ancestral condition (by assuming that a particular species diverged from the main stock prior to the development of this lamella) or a derived condition (by assuming that the absence of lamella is the result of secondary reduction of the feature).

TABLE 2

Percentage similarity matrix. (Figures taken to nearest 0·5%)

	elongatum	*calcator*	*fulvitarse*	*flaviscutellum*	*perornatum*	*ocypeta*	*nigricorne*	*amictum*	*scaposum*	*perniciosum*	*quodi*	*flavitarse*	*savaiiense*	*datanae*	*townesi*	*celeno*
calcator	80·0															
fulvitarse	87·5	95·2														
flaviscutellum	75·0	75·0	77·5													
perornatum	85·0	82·0	87·0	85·5												
ocypeta	77·0	84·0	90·0	87·0	87·0											
nigricorne	75·0	77·0	75·0	67·0	75·0	64·0										
amictum	85·0	85·0	85·0	75·5	85·5	69·0	92·5									
scaposum	77·5	85·0	82·5	77·5	82·5	74·0	87·0	87·0								
perniciosum	66·0	87·0	82·0	69·0	77·0	72·0	77·0	82·0	90·0							
quodi	67·0	70·0	72·5	65·0	77·5	67·0	83·0	85·0	87·0	84·0						
flavitarse	62·5	65·0	67·0	55·0	65·0	59·0	70·0	82·5	80·0	75·0	75·0					
savaiiense	72·0	74·0	79·0	72·0	82·0	76·0	62·5	72·5	74·0	68·0	64·0	64·0				
datanae	77·5	65·0	67·5	70·0	70·0	62·0	82·5	75·0	75·0	64·0	80·0	62·5	62·5			
townesi	72·0	67·0	75·0	72·0	72·0	74·0	65·0	75·0	75·0	67·0	70·0	50·0	60·0	62·5		
celeno	60·0	55·0	62·0	47·5	65·0	49·0	60·0	69·0	60·0	62·0	67·0	70·0	59·0	52·5	52·5	
aello	60·0	52·5	62·5	52·5	60·0	56·0	55·0	62·5	62·5	62·0	68·0	70·0	62·0	52·5	52·5	87·5

Consideration of the genus as a whole and its relationship to other genera has enabled the author to tentatively suggest that within *Heteropelma* the following may be considered to be ancestral character conditions.

1, flat clypeus without lateral projections;
2, absence of a pronotal hook;
3, presence of strongly impressed notauli;
4, possession of a complete mesosternal transcarina;
5, absence of lateral propodeal protuberances;
6, presence of a pair of subequal mid tibial spurs;
7, having the hind basitarsus less than 2·90 times as long as tarsus 2;
8, having the hind tarsal claws simply curved;
9. having the hind tarsal claws basally weakly lobate;
10, lacking an impressed area on the male tarsi;
11, having CI greater than 0·81;
12, having MI less than 2·00;
13, having the aedeagus terminally unequally bilobate;
14, having the occipital carina complete.

All these character conditions are found to occur frequently amongst the more primitive Therionini, that is amongst genera in which the cephalic capsule of the final instar larvae have discernible traces of hypostomal spurs. In the majority of Therionini the hypostomal spurs are entirely lost.

Using the method adopted by Gupta (1962) the index of divergence (i.e. number of derived characters) was calculated for each species of *Heteropelma* (Table 3). The position of the species was then shown in Chart 3 and the proposed phylogenies indicated by lines.

It is suggested that four species-groups exist. The largest of these, the *calcator*-group contains six species, *H. calcator*, *H. fulvitarse*, *H. elongatum*, *H. flaviscutellum*, *H. perornatum* and *H. ocypeta*. *H. townesi* is also believed to have been derived from this group, but because it is so widely geographically separated from the other species it has diverged morphologically and evolved a number of character conditions not found in other species (unicalcarate mid tibiae, high value of MI). All species in this group may be characterized by the possession of elongate hind basitarsi, simple clypeal structure, having the head weakly sexually dimorphic, etc. Within the group there are several very distinct specializations. *H. ocypeta* and *H. perornatum* show a tendency to develop strongly constricted heads. *H. elongatum* and *H. flaviscutellum* have apparently lost the impressed area on the male hind tarsi. (The reason for assuming these species have lost the impressed tarsal area whilst later assuming that *H. datanae* may either not have had or have lost a very long time ago such an impressed area are twofold. Firstly, some males of *H. fulvitarse*, which is morphologically very similar to *H. elongatum* and *H. flaviscutellum*, have a reduced tarsal impression, intermediate in form between those of *H. calcator* and *H. elongatum*. Secondly, the impressed area typically bears numerous flattened microtrichia which are often also present on ventro-distal

Table 3

Indices of divergence

SPECIES	CHARACTER CONDITION														INDEX OF DIVERGENCE
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
elongatum	0	1	0	0	0	0	1	1	1	0	1	0	1	0	6·0
calcator	0	1	0	0	0	0	1	1	1	1	1	0	1	0	7·0
fulvitarse	0	1	0	0	0	0	1	1	1	1	0·5	0	1	0	6·5
flaviscutellum	0	0	0	0	0	1	1	1	1	0	0	0	1	0	5·0
perornatum	0	1	0	0	0	0	1	1	1	1	0·5	0	1	0	6·5
ocypeta	0	1	0	0	0	1	1	1	1	1?	0	0	1?	0	7·0
nigricorne	1	1	0	0	0	0	1	1	1	1	0·5	0	1	0	7·5
amictum	1	1	0	0	0	0	0	0·5	0·5	1	1	0	1	0	6·0
scaposum	0	1	0	0	0	0	0	1	1	1	0·5	0	0	0	4·5
perniciosum	0	1	0	0	0	0	0	1	1	1?	0	0	0?	0	4·0
quodi	0	1	0	0	0	0	0	1	1	1	0	0	1	0	5·0
flavitarse	0	1	0	0	0	0	0	0	1	1	0	0	0	0	3·0
savaiiense	0	0	0	0	0	0	0	1	1	1	0	0	1	0	4·0
datanae	0	1	0	0	0	0	0	1	1	0	0	0	1	0	4·0
townesi	0	1	0	0	0	1	0·5	1	1	1	1	1	0	1	8·5
celeno	0	0	1	0	1	0	0	0	0	1	1	0	0	0	4·0
aello	0	0	1	1	1	0	0	0	0	1	0	0	1	0	5·0

(0 = ancestral character condition; 1 = advanced condition; 0·5 signifies an intermediate character condition)

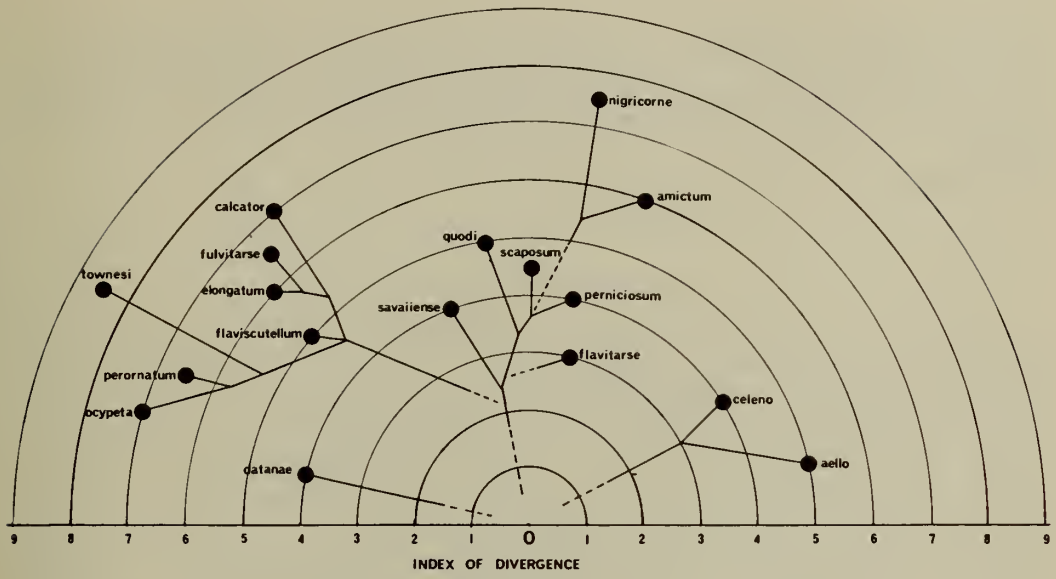


CHART 3. Proposed phylogenetic interrelationships of species of *Heteropelma*.

apex of the basitarsus. Flattened microtrichia are found on the tarsi of *H. elongatum* and *H. flaviscutellum* but have not been observed on the tarsi of *H. datanae*.)

The second and third species-groups are believed to be more closely interrelated than are either to the previously mentioned species-group. One of these, the *amictum*-group, contains only a pair of species characterized by the obviously swollen clypeus, relatively short basitarsus, etc. The second of these two groups, the *scaposum*-group, contains entirely Australasian species, *H. scaposum*, *H. perniciosum*, *H. quodi*, *H. savaiiense* and *H. flavitarse*. All these species except *H. savaiiense* have a bicoloured hind basitarsus. The group as a whole may be characterized by short basitarsus, simple clypeus, etc. Occasional specimens in this species-group have been observed to have a faint trace of lateral clypeal swellings. This and the similarity in form of the hind legs has been interpreted as indicative of a close phylogenetic relationship between this and the *amictum*-group.

A fourth species-group contains the two Papuan species, *H. celeno* and *H. aello*. These are distinct from all other species in a large number of features including propodeal shape, form of tarsal claws, absence of pronotal hook, etc. The affinities of these species are not clear but they do not appear to be at all closely related to the other Australasian species which all belong in the *scaposum*-group. Certain features of the *celeno*-group seem to indicate that it diverged from the main stock of the genus a considerable time ago. The structure of the aedeagus, form of the posterior transcarina of the mesosternum, and shape and coloration of the female face are reminiscent of those of *Therion* species. These two species may possibly be rather specialized descendants of species which diverged from the main *Heteropelma* stock shortly after *Heteropelma* and *Therion* separated. Far more evidence

is needed, however, before any reliable statements can be made concerning the position of this species-group. It would be of particular interest to examine the first instar larva of these species as considerable differences are known to exist between the first instar larvae of *Therion* and *Heteropelma* (Plotnikov, 1914; Tothill, 1922).

The position of *H. datanae* is unclear at present.

ACKNOWLEDGEMENTS

I would like to thank the Keeper of Entomology, British Museum (Natural History) for providing study facilities and Mr L. A. Mound and Dr M. G. Fitton for their cooperation. I am grateful to the following persons and institutions for loan of material: Miss J. Cardale, ANIC, Canberra, Australia; Dr R. W. Carlson, USNM, Washington, U.S.A.; Dr E. C. Dahms, QM, Fortitude Valley, Australia; Dr P. Dessart, IRSNB, Brussels, Belgium; Mrs C. N. Higa, BPBM, Honolulu, U.S.A.; Dr D. R. Kasparyan, ZI, Leningrad, U.S.S.R.; Dr D. Kitchener, WAM, Perth, Australia; Mme S. Kellner-Pillault, MNHN, Paris, France; Dr E. Kierych, IZPAN, Warsaw, Poland; Dr J. Oehlke, DEI, Eberswalde, D.D.R.; Mr C. O'Toole, UM, Oxford; Dr J. Papp, TM, Budapest, Hungary; Mr E. C. Pelham-Clinton, RSM, Edinburgh, Scotland; Dr M. Suwa, EIHU, Hokkaido, Japan and Dr H. K. Townes, Ann Arbor, U.S.A.

I would like to thank Dr Townes, Dr Fitton and colleagues on the staff of the CIE and BMNH for their advice and cooperation at various stages and for their many helpful criticisms. I am grateful to Miss P. Mitchell for her assistance at various stages and for typing the manuscript.

REFERENCES

Ashmead, W. H. 1900. Hymenoptera. *In* Smith, J. B., *Insects of New Jersey* (1899) : 501–613. Trenton.

Barbey, A. 1927. La fidonie du pin dans les pineraies d'Alsace et de Lorraine. *Rev. Eaux et Forêts* Dec. **1926** : 1–7, 6 pls.

Betrem, J. G. & Bradley, J. C. 1971. The African Campsomerinae. *Monografieën ned. ent. Vereen.* **6** : 1–326, 6 pls, 52 figs.

Brauns, S. 1898. Die Ophionoiden. *Arch. Ver. Freunde Naturg. Mecklenb.* **43** : 58–72.

Brullé, A. 1846. Hymenoptera. *In* Lepeletier de Saint-Fargeau, A. L. M., *Histoire Naturelle des Insectes*, Hyménoptères 4, (1) 680 pp. Paris.

Cameron, P. 1899. Hymenoptera Orientalia 8. The Hymenoptera of the Khasia Hills. *Mem. Proc. Manchr lit. phil. Soc.* **43**(1) : 1–220.

—— 1902. On Hymenoptera collected by Mr Robert Shelford at Sarawak and on Hymenoptera of the Sarawak Museum. *J. Straits Brch R. Asiat. Soc.* **37** : 29–140.

—— 1906. A new genus and five new species of Ichneumonidae from Australia. *Entomologist* **39** : 180–183.

—— 1907. A contribution to the knowledge of the Hymenoptera of the Oriental region. *Ann. Mag. nat. Hist.* (7) **20** : 10–30.

Ceballos, G. 1963. Los Anomalinos de España. *Graellsia* **20** : 55–67, 4 figs.

CONSTANTINEANU, M. I. & PETÇU, I. P. 1969. Therioninae (Hym. Ich.) de la zone du Futur Lac d'accumulation de Portile de Fier (Roumanie). *Anal. Stiint. Univ. Al. I. Cuza* **15** : 93–101, 12 figs.

CROWSON, R. A. 1970. *Classification and Biology*. vii + 350 pp. London.

CUSHMAN, R. A. 1937. H. Sauter's Formosan Collection: Ichneumonidae. *Arb. morph. taxon. Ent. Berl.* **4** : 283–312.

DESVIGNES, T. 1856. *Catalogue of British Ichneumonidae in the collection of the British Museum*. 120 pp. London.

DUTT, G. R. 1923. An annotated list of Ichneumonidae in the Pusa collection. *Mem. Dep. Agric. India* (Ent.) **8** : 13–27.

EADY, R. D. 1968. Some illustrations of microsculpture in Hymenoptera. *Proc. R. ent. Soc. Lond.* (A) **43** : 66–72.

ENDERLEIN, G. 1921. Beiträge zur Kenntnis aussereuropäischer Ichneumoniden. *Stettin. ent. Ztg* **82** : 1–45.

EVANS, H. E. 1968. Studies on Neotropical Pompilidae (Hymenoptera) IV. Examples of dual sex-limited mimicry in *Chirodamus*. *Psyche, Camb.* **75** : 1–22, 21 figs.

FABRICIUS, J. C. 1775. *Systema entomologiae sistens insectorum classes, ordines, genera, species etc.* 832 pp. Flensburgi et Lipsiae.

—— 1798. *Supplementum Entomologiae systematicae*. 572 pp. Halfniae.

FITTON, M. G. 1976. The western Palaearctic Ichneumonidae (Hymenoptera) of British authors. *Bull. Br. Mus. nat. Hist.* (Ent.) **32** : 301–373.

FOERSTER, A. 1868. Synopsis der Familien und Gattungen der Ichneumoniden. *Verh. naturh. Ver. preuss. Rheinl.* **25** : 135–221.

FRIEDRICHS, K., SCHAERFFENBERG, B. & STURM, H. 1941. Ueber die Feinde des Kiefernspanners mit Berücksichtigung des Mischwaldes. *Z. angew. Ent.* **27** : 621–641.

FULLAWAY, D. T. 1940. New species from the Bishop Museum collection of Samoan parasitic Hymenoptera. *Proc. Hawaii. ent. Soc.* **10** : 399–411.

GAULD, I. D. 1973. Notes on some Anomaloninae (Hymenoptera: Ichneumonidae) on Cannock Chase during August, 1973. *Entomologist's Gaz.* **24** : 304.

—— 1974. Notes on the species of *Heteropelma* Wesmael (Hym. Ich.) occurring in Australia. *Bull. ent. Res.* **64** : 541–544.

—— 1976. The classification of the Anomaloninae (Hymenoptera: Ichneumonidae). *Bull. Br. Mus. nat. Hist.* (Ent.) **33** : 1–135.

GORNITZ, K. 1931. Festellung von Parasitenlarven in den Puppen des Kiefernspanners. *Anz. Schädlingsk.* **7** : 30–33.

GRAVENHORST, J. L. C. 1829. *Ichneumonologia Europaea*. **3** : 1097 pp. Vratislaviae.

GUPTA, V. K. 1962. Taxonomy, zoogeography and evolution of Indo-Australian *Theronia* (Hym. Ich.). *Pacif. Insects Monogr.* **4** : 1–142, 29 figs, 15 maps.

HASEMAN, L. 1940. The walnut caterpillar. *Bull. Mo. agric. Exp. Stn.* **418** : 1–14, 11 figs.

HEDQVIST, K. J. 1949. Några iakttagelser över tall mätarens parasiter under senaste härjningen i södra och mellersta Sverige (1943–1945). *Medd. Skogsforskningsinst.* **37**(3) : 1–18.

HUXLEY, J. 1939. Clines: an auxillary method in taxonomy. *Bijdr. Dierk.* **27** : 491–520.

IWATA, K. 1958. Ovarian eggs of 233 species of Japanese Ichneumonidae. *Acta hymenopt., Tokyo* **1** : 63–78, 233 figs.

—— 1960. Comparative anatomy of the ovary in Hymenoptera. Part 5. Ichneumonidae. *Acta hymenopt., Tokyo.* **1** : 115–171, 137 figs.

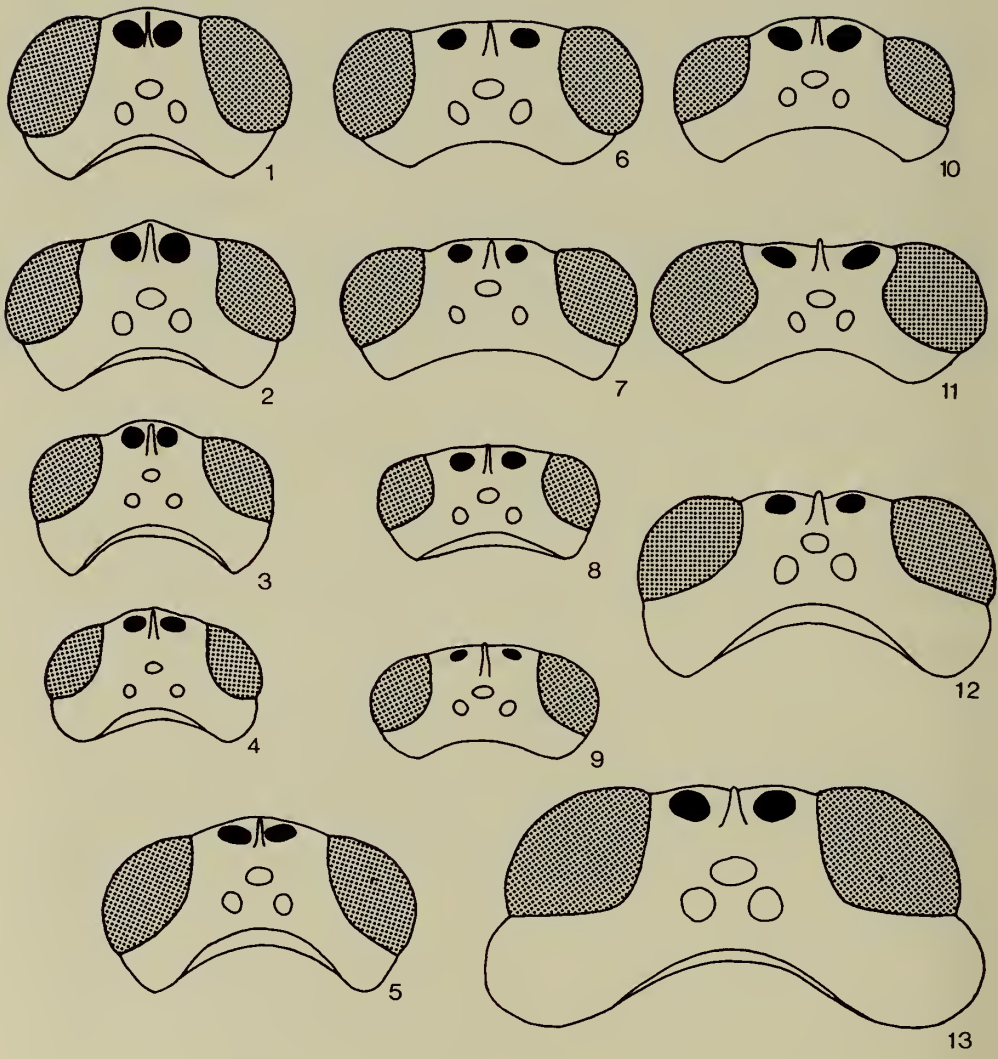
LJUNGDAHL, D. 1916. Några lepidopterologiska anteckninger och puppbeskrivningar samt en del parasitekelynd. *Ent. Tidskr.* **1916** : 70–94, 34 figs.

MALYSHEVA, M. S. 1960. The effect of dusting by aircraft on the abundance of the pine Geometrid & its parasites. [In Russian]. *Trud. vsesoyuz. Inst. Zasch. Rast.* **15** : 41–56.

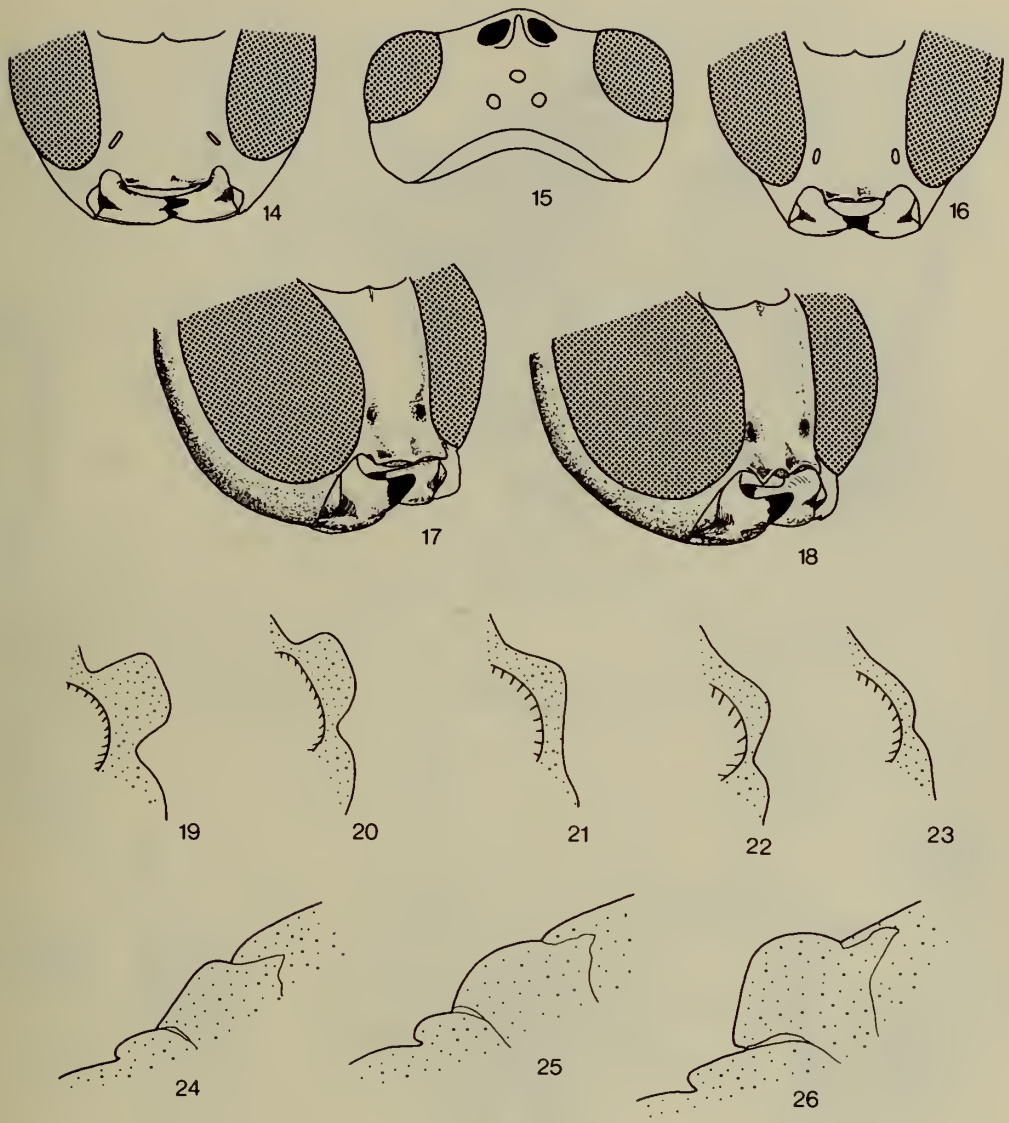
—— 1962. The pine looper (*Bupalus piniarius* L.) and its natural enemies in the conditions of the Savala forest district in the Voronezh region. [In Russian.] *Ent. Obozr.* **41** : 532–544, 4 figs.

MATSUMURA, S. 1918. *Thousand insects of Japan.* Supplement 4. 247 pp., 13 pls. Tokyo.
—— 1926. On the 3 species of *Dendrolimus* (Lepidoptera) which attack spruce and fir trees in Japan, with their parasites and predaceous insects. *Ezheg. zool. Muz.* **26** : 27–50.
MEYER, N. F. 1935. *Tables systématiques des hyménoptères parasites de l'URSS et des pays limitrophes* **4**. [In Russian.] 535 pp. Leningrad.
MORLEY, C. 1913*a*. *Revision of the Ichneumonidae* 2. 144 pp. London.
—— 1913*b*. *The fauna of British India including Ceylon and Burma.* Hymenoptera 3, Ichneumonidae. 513 pp. London.
—— 1914. Hymenoptera 4: Ichneumonidae. *Rec. Indian Mus.* **8** : 323–328.
—— 1915. *The Ichneumons of Gt Britain* **5**. x + 400 pp. London.
NORTON, E. 1863. Catalogue of our species of *Ophion, Anomalon, Paniscus & Campoplex. Proc. ent. Soc. Philad.* **1** : 357–368.
PECK, O. 1937. The male genitalia of Hymenoptera, especially the Ichneumonidae. *Can. J. Res.* **15** (D) 12 : 221–274, 158 figs.
PERKINS, J. F. 1953. Notes on the British Ichneumoninae with descriptions of new species. *Bull. Br. Mus. nat. Hist.* (Ent.) **3** : 105–176, 41 figs.
PLOTNIKOV, V. 1914. Contribution à la biologie de *Bupalus piniarius* L. (Lep. Geom.) et de quelques uns de ces parasites. [In Russian.] *Ent. Obozr.* **14** : 23–43, 8 figs.
RICHARDS, O. W. 1956. Hymenoptera: introduction and key to families. *Handbk Ident. Br. Insects.* **6**(1) : 1–91, xxii + 197 figs.
RILEY, C. V. 1888. The habits of *Thalessa* and *Tremex. Insect Life* **1**(6) : 168–179, 5 figs.
RITZEMA, B. J. 1920. De gestreepte Dennenrups (*Trachea piniperda* Panz. *Panolis griseovariegata* Goeze). *Tijdschr. Plziekt.* **26** : 28–60.
SCHAFFNER, J. V. & GRISWOLD, C. L. 1934. Macrolepidoptera and their parasites reared from collections in the north-eastern part of the United States. *Misc. Publs. U.S. Dep. Agric.* no. 188 : 1–160.
SCHMIEDEKNECHT, O. 1908. *Opuscula Ichneumonologica* **18** : 1407–1520. Blankenburg i Thuringen.
—— 1935. *Opuscula Ichneumonologica* Suppl. 24 : 5–84. Blankenburg i Thuringen.
—— 1936. *Opuscula Ichneumonologica* Suppl. 25 : 85–140. Blankenburg i Thuringen.
SEITNER, M. 1922. Der Kiefernspanner in Galizien 1915–1917 eine Tafel. *Zentbl. ges. Forstw.* **47** : 198–213.
SHESTAKOV, A. 1923. Ad cognitum specierum tribus Anomalonini (Hym., Ichneumonidae) *Ezheg. zool. Muz.* **24** : 44–51.
SITOWSKI, L. 1922. Zu biologji poprocha cetyniaka (*Bupalus piniarius* L.) w puszczy Sandomierskiej. *Pr. Nauk. Uniw. Poznan. Sekcja Rolniczo-Leśna* **2** : 1–9, 4 pls.
SHORT, J. R. T. 1959. A description and classification of the final instar larvae of the Ichneumonidae (Insecta; Hymenoptera). *Proc. U.S. natn. Mus.* **110** : 391–511, 64 figs.
—— 1970. On the classification of the final instar larvae of the Ichneumonidae (Hymenoptera). Supplement. *Trans. R. ent. Soc. Lond.* **122** : 185–210, 16 figs.
STEINER, P. 1932. Zur Kenntnis der Parasiten des Kiefernspanners. *Z. angew. Ent.* **17** : 601–630, 7 figs.
SZÉPLIGETI, G. V. 1905. *In* Wytsman, P., *Genera Insectorum:* Hymenoptera, Ichneumonidae **34** : 1–68. Bruxelles.
—— 1906. Neue exotische Ichneumoniden der Sammlung des Ungarischen National-Museums. *Annls hist.-nat. Mus. natn. hung.* **4** : 119–156.
TOTHILL, J. D. 1922. The natural control of the Fall Webworm in Canada. *Bull. Dep. Agric. Can. ent. Brch.* **19** : 1–107, 99 figs.
TOWNES, H. K. 1940. A revision of the Pimplini of eastern North America (Hym. Ich.). *Ann. ent. Soc. Am.* **33** : 283–323.
—— 1945. A catalogue and reclassification of the Nearctic Ichneumonidae 2. *Mem. Am. ent. Soc.* **11** : 479–923.
—— 1951. *In* Muesebeck, Krombein, Townes & others. Hymenoptera of America North of Mexico – a synoptic catalogue. *Agriculture Monogr.* **2** : 1–1420.

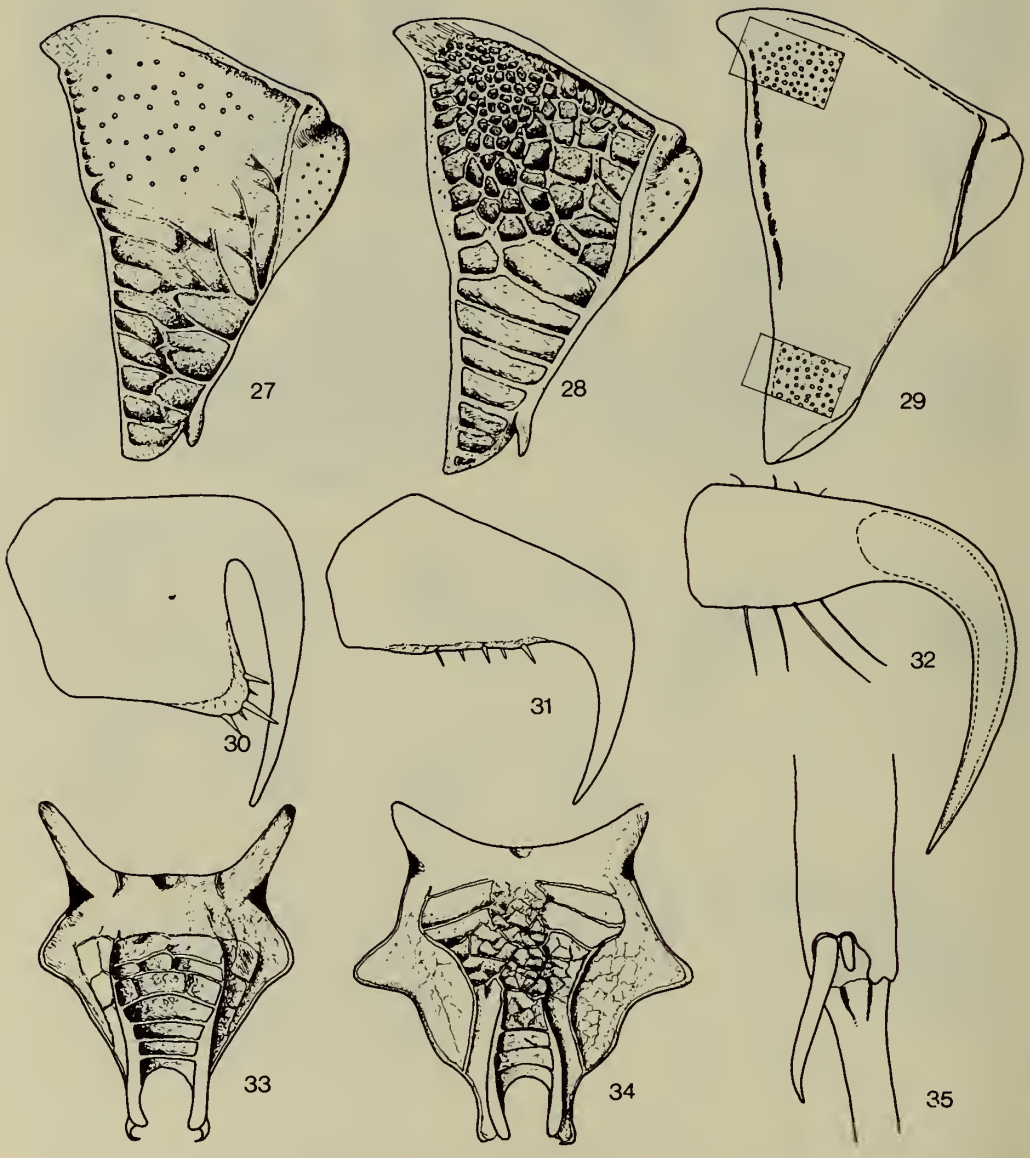
—— 1957. Nearctic wasps of the subfamilies Pepsinae and Ceropalinae. *Bull. U.S. natn. Mus.* **209** : 1–286, 161 figs.
—— 1971. The genera of Ichneumonidae. *Mem. Am. ent. Inst.* **17** : 1–372, 217 figs.
—— & Chiu S-C. 1970. The Indo-Australian species of *Xanthopimpla*. *Mem. Am. ent. Inst.* **14** : 1–372, 465 figs.
—— Momoi, S. & Townes, M. 1965. A catalogue and reclassification of eastern Palaearctic Ichneumonidae. *Mem. Am. ent. Inst.* **5** : 1–661.
—— Townes, M. & Gupta, V. K. 1961. A catalogue and reclassification of Indo-Australian Ichneumonidae. *Mem. Am. ent. Inst.* **1** : 1–522.
Turner, R. E. 1919. Notes on the Ichneumonidae in the British Museum 1. *Ann. Mag. nat. Hist.* (9) **3** : 550–558.
Uchida, T. 1928. Zweiter Beitrag zur Ichneumoniden-Fauna Japans. *J. Fac. Agric. Hokkaido Imp. Univ.* **21** : 177–297, 71 figs.
—— 1953. Die Insekten Fauna aus dem Berg Ishizuchi und dem Tal Omogo. *Trans. Shikoku ent. Soc.* **3** : 126–131.
—— 1958. Anomalinen und Therionen in der Sammlung des Entomologischen Instituts der Hokkaido Universitaet 1. *Insecta matsum.* **21** : 85–108.
Vachal, J. 1907. Hyménoptères de la Nouvelle Calédonie. *Revue Ent.* **26** : 113–123.
Viereck, H. L. 1917. *Guide to the Insects of Connecticut; Part 3, The Hymenoptera or wasp-like insects of Connecticut.* 824 pp., 10 pls. Hartford.
Wesmael, C. 1849. Revue des Anomalons de Belgique. *Bull. Acad. r. Belg.* (2) **16** : 115–139.



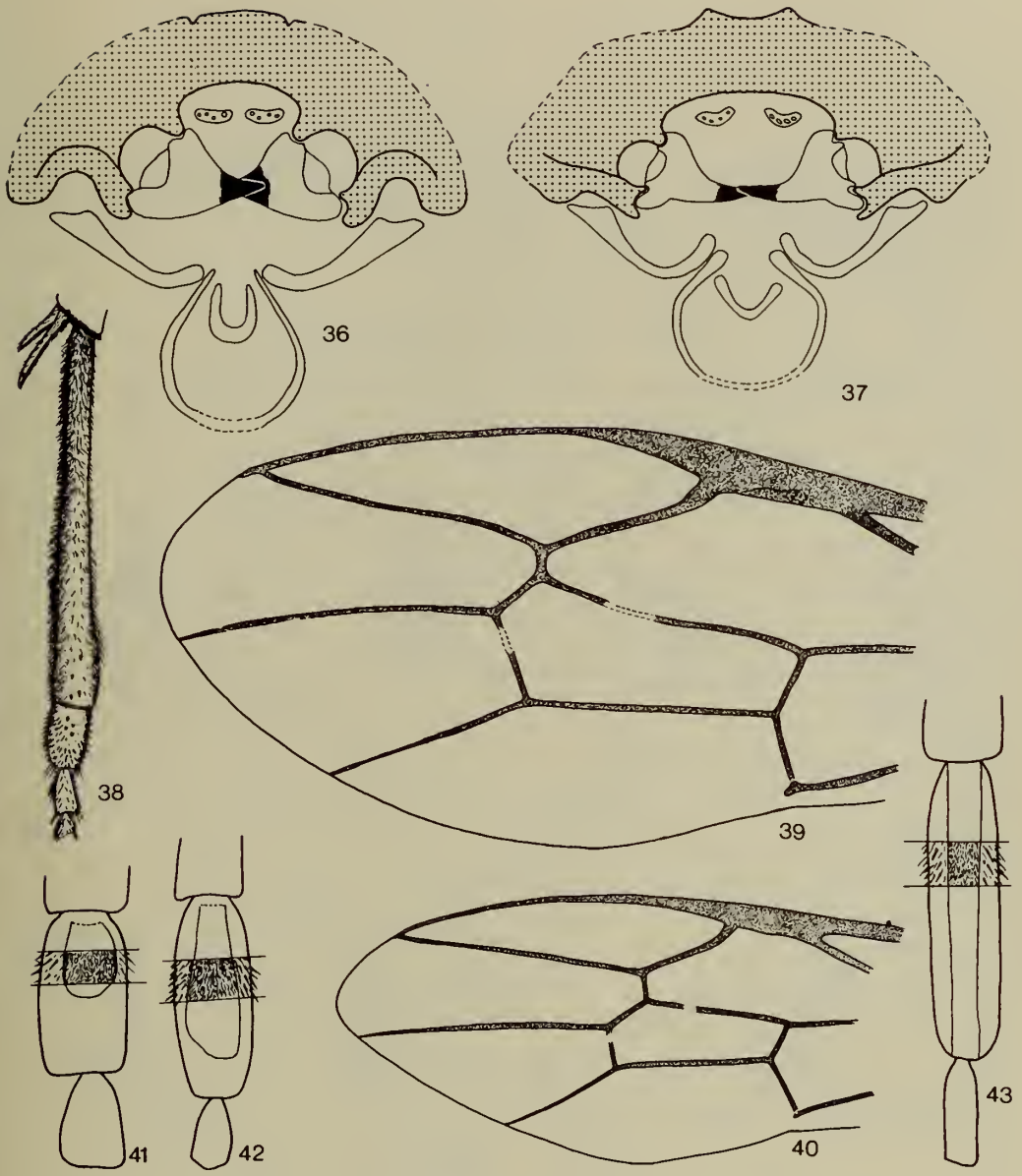
FIGS 1–13, heads, dorsal view. 1, *Heteropelma fulvitarse* Cameron, ♂; 2, *H. fulvitarse* Cameron, ♀; 3, *H. calcator* Wesmael, ♂; 4, *H. calcator* Wesmael, ♀; 5, *H. elongatum* Uchida, ♂; 6, *H. perornatum* (Cameron), ♀; 7, *H. quodi* (Vachal), ♀; 8, *H. townesi* sp. n., ♂; 9, *H. savaiiense* (Fullaway), ♂; 10, *H. ocypeta* sp. n., ♀; 11, *H. celeno* sp. n., ♀; 12, 13, *H. amictum* (Fabricius), ♂, (12) normal, (13) 'buccate-headed'.



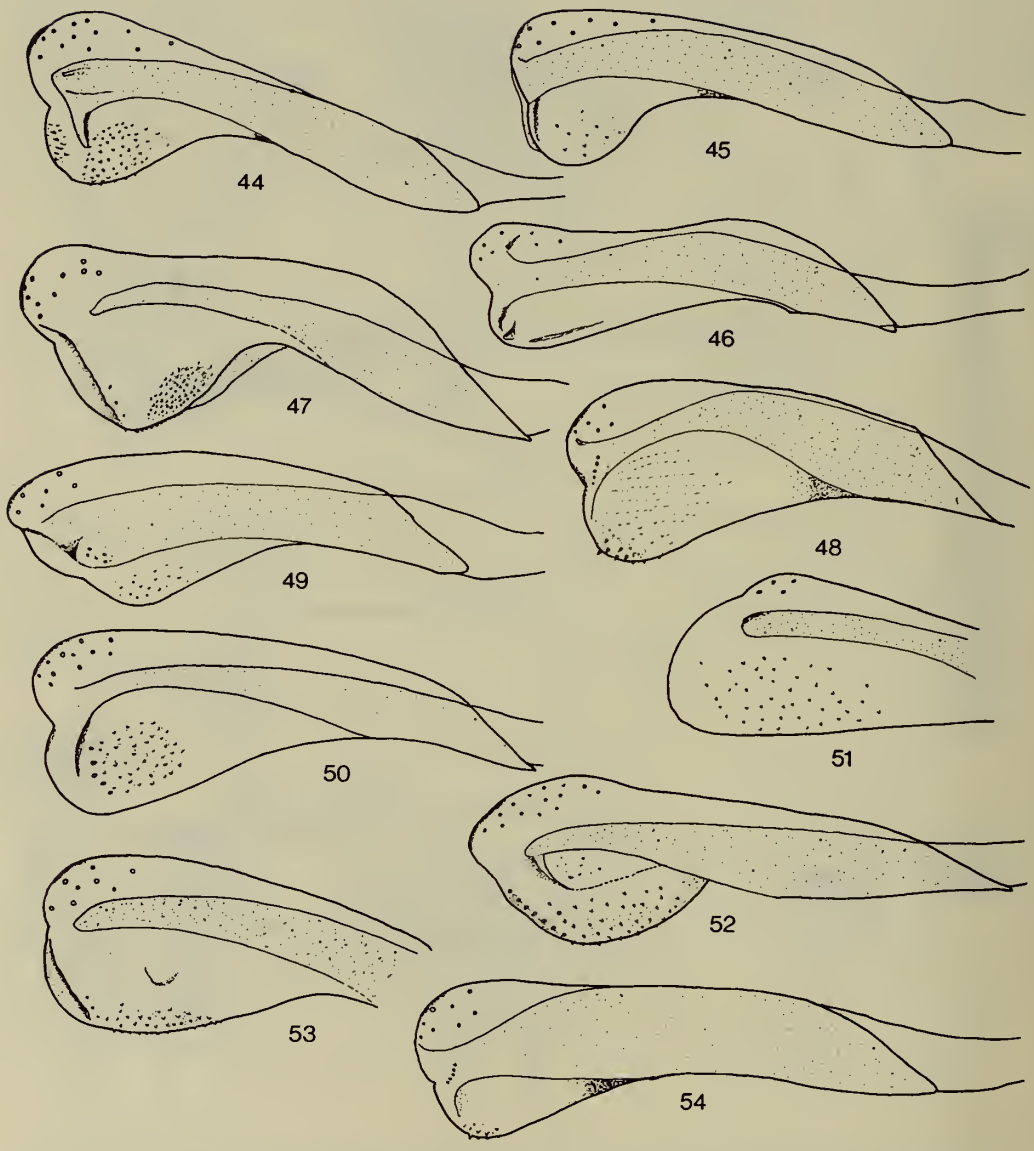
FIGS 14, 15, *Heteropelma nigricorne* (Szépligeti), ♀. 14, lower face, anterior view; 15, head, dorsal view. FIGS 16–18, *H. amictum* (Fabricius), ♀. 16, lower face, anterior view (showing weakly laterally protruding clypeus); 17, the same, antero-lateral view; 18, lower face, antero-lateral view (showing strongly laterally protruding clypeus). FIGS 19–23, interantennal lamella in profile. 19, *H. calcator* Wesmael, ♀; 20, *H. fulvitarse* Cameron, ♀; 21, *H. perornatum* (Cameron), ♀; 22, *H. elongatum* Uchida, ♂; 23, *H. flaviscutellum* Uchida, ♂. FIGS 24–26, scutellum in profile. 24, *H. perornatum* (Cameron), ♂; 25, *H. savaiiense* (Fullaway), ♂; 26, *H. datanae* Riley, ♂.



FIGS 27–29, pronotum, lateral view. 27, *Heteropelma perornatum* (Cameron), ♀; 28, *H. fulvitarse* Cameron, ♀; 29, *H. celeno* sp. n., ♀. FIGS 30–32, ♀ hind tarsal claw; 30, *H. scaposum* (Morley); 31, *H. flavitarse* Brullé; 32, *H. celeno* sp. n. FIGS 33, 34, ♀ propodeum, dorsal view. 33, *H. celeno* sp. n.; 34, *H. aello* sp. n. FIG. 35, *H. ocypeta* sp. n., apex of mid tibia, internal view.



Figs 36, 37, cephalic capsule of final instar larvae, anterior view. 36, *Heteropelma calcator* Wesmael; 37, *H. scaposum* (Morley). Fig. 38, *H. flaviscutellum* Uchida, ♂ hind tarsi I–IV, ventral view. Figs 39, 40, left forewings, distal part. 39, *H. savaiiense* (Fullaway); 40, *H. townesi* sp. n. Figs 41–43, ♂ hind tarsi II & III, ventral view (detail of pubescence shown only in part). 41, *H. fulvitarse* Cameron; 42, *H. amictum* (Fabricius); 43, *H. townesi* sp. n.



FIGS 44–54, apices of aedeagi, lateral view. 44, *Heteropelma perornatum* (Cameron); 45, *H. quodi* (Vachal); 46, *H. amictum* (Fabricius); 47, *H. celeno* sp. n.; 48, *H. calcator* Wesmael; 49, *H. scaposum* (Morley); 50, *H. elongatum* Uchida; 51, *H. townesi* sp. n.; 52, *H. fulvitarse* Cameron; 53, *H. aello* sp. n.; 54, *H. datanae* Riley.

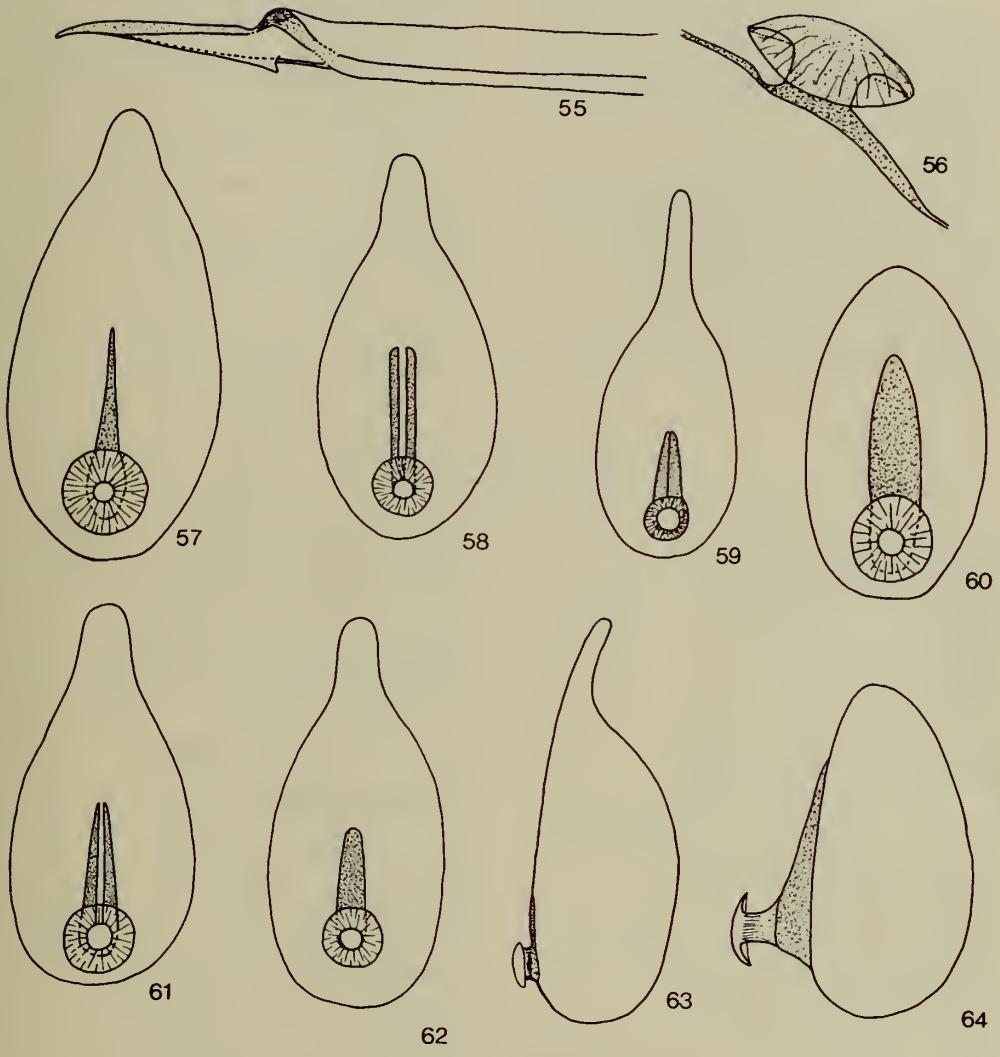


FIG. 55, apex of valvula 2, lateral view. *Heteropelma fulvitarse* Cameron. FIGS 56–64, ovarian eggs; 56, *H. celeno*, detail of 'sucker'; 57, *H. celeno* sp. n., dorsal view; 58, *H. perornatum* (Cameron), dorsal view; 59, *H. calcator* Wesmael dorsal view; 60, *H. scaposum* (Morley), dorsal view; 61, *H. amictum* (Fabricius), dorsal view; 62, *H. fulvitarse* Cameron, dorsal view; 63, *H. calcator* Wesmael, lateral view; 64, *H. scaposum* (Morley), lateral view.

INDEX TO RECORDED HOSTS

INDEX TO PARASITES

Synonyms are in *italics*; principal references are in **bold.**

I. D. Gauld, L.I.Biol.
Commonwealth Institute of Entomology
c/o British Museum (Natural History)
Cromwell Road
London SW7 5BD